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Complex Algal Dynamics and Optimal Control with Algicidal Activity and Reabsorption of Algal Cell Contents

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Abstract

Algaecides utilizing bacteriolytic algae are considered as a promising approach for algae control. These bacteria inhibit the continuous reproduction of algae cells in various ways, including lysing the cells, which leads to the release of cellular contents and affects the levels of nitrogen and phosphorus in the environment. In this paper, we establish a novel mathematical model with algicidal activities and the reabsorption of algal cell contents. The model exhibits complex dynamical phenomena: (i) backward and forward bifurcations; (ii) transcritical bifurcation and saddle-node bifurcation discussed via Sotomayor's theorem; (iii) Hopf bifurcation; (iv) the codimension 2 bifurcations, exemplified by the Bogdanov-Takens bifurcation, via the methodologies of normal form theory and the center manifold theorem. We also obtain an explicit formula for the ultimate lower bound of algal bloom. Sensitivity analysis of the basic ecological reproductive indices R_0 is conducted, and the optimal control problem is formulated by integrating environmental factors and physical algal control methods. The analysis indicates that using algicidal bacteria to lyse algal cells can result in two scenarios: algicidal dominance and nutrient supplementation dominance. The former effectively curbs the sustained reproduction of algal cells and is more effective than physical algal control methods.

Keywords Algal bloom · Algicidal bacteria · Bifurcation analysis · Stability analysis · Optimal control

Mathematics Subject Classification $\ 92B05 \cdot 92D40 \cdot 34D20 \cdot 34C23$

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1 Introduction

Phytoplankton are ubiquitous photosynthetic organisms found in marine, coastal, and inland water bodies. As the primary producers in the ocean, they play a crucial role in maintaining the stability and health of marine ecosystems. Nitrogen and phosphorus serve as essential nutrients for algae growth and are present in aquatic systems in various forms, including dissolved inorganic nutrients, dissolved organic nutrients, granular organic nutrients, and biologically bound nutrients (Hu et al. 2010). The development and expansion of the marine industry have led to a rapid increase in the concentration of nitrogen and phosphorus resources in water. This excessive nutrient content can adversely affect algae reproduction and trigger algal blooms. These toxic microalgae blooms result in a decrease in dissolved oxygen and water transparency, and they also release toxins that can cause massive deaths of fish, mollusks, and other marine life (Kang et al. 2005). In recent years, the scale and frequency of harmful algal blooms have been increasing, resulting in significant negative impacts on aquatic environments, human health, and socio-economic development (Gobler 2019; Griffin 2017). Harmful algal blooms represent a complex ecological phenomenon, and managing these blooms necessitates a multifaceted approach that encompasses chemical, physical, and biological methods. Research and governance efforts focus on developing systems and strategies that specifically target pest species while minimizing harm to the environment and other aquatic organisms (Amin et al. 2012; Shannon et al. 2008). Among these methods, biotechnological algae treatment has received significant advancements due to its low environmental toxicity and biodegradability (Hargraves 2008; Pichierri et al. 2017).

It is widely known that a unique microecological environment system can be formed by algae and certain algicidal bacteria. Dakhama et al. discovered that Pseudomonas aeruginosa exhibits a potent inhibitory effect on the growth of green microalgae and cyanobacteria through the release of low molecular weight and heatresistant factors (Dakhama et al. 1993). Salomon et al. discovered 5 strains, isolated from the Baltic Sea, that are associated with α and γ Proteobacteria and the Firmicutes phylum, and these strains demonstrate inhibitory effects on the growth of cyanobacteria. Furthermore, 8 other strains isolated showed either positive effects or no effects on cyanobacterial growth (Salomon et al. 2003). Thus, the interaction between algae and algicidal bacteria resembles algal symbiosis. It has been reported that numerous algicidal bacteria have been isolated and exhibit high inhibition rates against harmful algae. For example, Hare identified a bacterium called Shewanella IRI-160 that has an inhibitory effect on the growth of a variety of dinoflagellates (Hare et al. 2005). The crude ethyl acetate extract of marine bacteria HSB07 has certain inhibitory activity on the red tide algae Gymnodinium sp. (Liu et al. 2013). Marine bacteria Thalassospira ZR-2 and the benzoic acid produced by them have algicidal activity on harmful algal bloom species Karenia mikimotoi (Lu et al. 2016). Algicidal bacteria are diverse and widely distributed in soil and water environments. Yamamoto et al. isolated an actinic strain with high algae-solubilizing ability from the bottom mud of a eutrophic lake (Yamamoto et al. 1998). Zheng et al. isolated the O4-6 strain from sediments in the Fujian Yunxiao National Mangrove Nature Reserve, which has been demonstrated significant algicidal activity against harmful algal bloom species (Zheng et al. 2012).

Fukami et al. isolated the bacterium 5N-3 from the Uragami Sea in Kochi Prefecture, Japan, which significantly inhibits the growth of *Gymnodinium nagasakiense* (Fukami et al. 1992). Imamura et al. isolated a strain of Sphingomonas with high efficiency in degrading Microcystis aeruginosa from Lake Biwa in Japan Imamura et al. (2001). Therefore, the interplay between algae and bacteria offers the potential for utilizing algicidal bacteria as a biological control measure against harmful algal blooms. The mechanism of inhibiting algal growth by algicidal bacteria can be divided into direct action and indirect action. Li et al. found and verified for the first time that the strain Altererythrobacter sp. LY02 has indirect algicidal activity against the toxic algae Alexandrium tamarense, and the active substances secreted by the strain can effectively control harmful algal blooms (Li et al. 2016). Besides, Bidle and Falkowski found that heterotrophic bacteria can feed on resources secreted by phytoplankton cells or released after algal cells die and lyse (Bidle and Falkowski 2004). Currently, numerous biological studies have delved into the intricate interplay between algae and bacteria, yet there remains a notable absence of scientific methodologies for quantifying algal bloom management strategies. Consequently, mathematical modelling could offer a novel analytical approach to investigate the dynamic mechanisms underlying the interaction between algae and algicidal bacteria.

Nitrogen and phosphorus serve as vital nutrients for the growth of algal cells. Phosphorus is a critical component of various biochemical substances in algal cells, including nucleic acids, cell membranes, and ATP, and it plays a vital role in nitrogen metabolism within these cells (Merchant and Helmann 2012; Orchard et al. 2009). Furthermore, phosphorus participates in a multitude of metabolic processes within algae, facilitating the synthesis, transformation, and transport of carbohydrates, ultimately contributing to the optimal growth of the algae. The effect of phosphorus is also related to nitrogen, and phosphorus can not achieve a good effect when nitrogen is short (Orchard et al. 2009; Taiz and Zeiger 1998). Therefore, to achieve longterm and effective management of harmful algal blooms, it is imperative to minimize both phosphorus and nitrogen inputs (Havens et al. 2003; Paerl et al. 2001. In recent decades, researches have primarily focused on controlling eutrophication, predicting algae blooms, simulating algae dispersion trends, and formulating eutrophication control strategies based on actual data. Malmaeus and Håkanson optimized existing models for predicting phosphorus concentration and eutrophication effects in lake ecosystems, providing significant differences and improving prediction capabilities (Malmaeus and Håkanson 2004). Wang et al. studied the influence of environmental factors on algal growth and nutrient threshold of harmful algal blooms, and proposed the key role of nitrogen and phosphorus interaction and optimal nitrogen and phosphorus mass ratio in algal reproduction (Wang et al. 2015). Zhang et al. developed a mathematical model linking surface and deep water layers in lakes to describe phytoplankton competition for nutrients and light in stratified lakes. They analyzed stability and critical thresholds, providing a theoretical basis for predicting phytoplankton competition and blooms (Zhang et al. 2021). Heggerud et al. investigated the growth dynamics of cyanobacteria under nutrient limitation using a multiscale analysis approach. They uncovered the driving mechanisms at different growth stages and predicted the duration of cyanobacterial blooms, offering new insights into the application of multiscale methods in nutrient ratio models (Heggerud et al. 2020).

Cui and Lawson proposed a single-population model to explain the effects of resource constraints on the growth of single-population organisms (Cui and Lawson 1982). The application of mathematical models for estimating the progression of harmful algal blooms and assessing the feasibility of algal control measures extends beyond the solitary factor of nutrient intake control. Gazi et al. analyzed the structural stability of a tropical bloom ecosystem by constructing a two-dimensional nonlinear differential equation model (Gazi and Das 2010).

Furthermore, the creation and examination of mathematical models offer valuable assistance in developing strategies for algae control across various domains (Heggerud et al. 2024). In terms of physical algae removal, fishing stands as the most prevalent method for controlling algae. Pankaj et al. introduced a mathematical model encompassing 17 interactions between nutrients, algae, detritus, and bacteria, highlighting that consistent removal of detritus plays a crucial role in the revitalization of lake ecosystems (Tiwari et al. 2019). Flocculants have also been suggested as a means to manage and control algal blooms. In 1917, Smoluchowski introduced the initial viable flocculation model, demonstrating its ability to accurately predict the condensation behavior of colloidal solutions through rigorous theoretical deduction and sophisticated mathematical modeling (Smoluchowski 1917). Additionally, some researchers have developed mathematical models to simulate the algae control process using microbial flocculants (Wang et al. 2018). From an economic perspective, both fishing and physical flocculation require substantial human and material resources, and the recovery of the ecosystem is a lengthy process. Hence, finding a swift and effective algal control method that poses minimal environmental harm is a pressing issue that requires immediate attention. In the biological realm, numerous microorganisms have been suggested as potential inhibitors of algal cell reproduction.

Microorganisms can achieve algae control through diverse methods, including disrupting algal cell structure, inhibiting algal photosynthesis, interfering with algal genetic expression, and flocculating algal cells (Gumbo and Cloete 2011; Shi et al. 2006; Sun et al. 2015; Xuan et al. 2017). These algicidal approaches alter the aquatic environment to varying degrees, which in turn affects the efficacy of algae control. Wang et al. constructed a bacteria-algae interaction model to explore the impact of carbon and phosphorus limitations on their growth. They outlined three dynamic scenarios and demonstrated the competitive edge of bacteria with low nucleic acid content under phosphorus-limited conditions (Wang et al. 2007). To the best of our knowledge, very few existing mathematical models specifically address the algicidal mechanisms of algicidal bacteria. We aim to propose a novel ordinary differential equation model to investigate the indirect algicidal process, where we investigate how the contents of algae cells, released after being lysed by algicidal bacterial secretions, affect the levels of nitrogen and phosphorus in the environment. This approach allows us to understand the sensitive and significant impacts of algae cell contents on environmental changes. Furthermore, our model incorporates the nutrient recycling process, where the contents of lysed algal cells replenish the aquatic system and are subsequently utilized by surviving algal cells, enabling us to assess the algae-inhibiting efficacy of algicidal bacteria that operate through such mechanisms.

The rest of this paper is organized as follows. Section 2 aims to formulate a mathematical model of algae-algicidal which includes nitrogen, phosphorus and algi-



Fig. 1.1 Schematic diagram of system (2.1)

cidal bacteria. Section 3 conducts dynamic analysis of the system, including the existence of algae-free equilibrium and algae-present equilibrium, the existence of backward and forward bifurcations, transcritical bifurcation, saddle-node bifurcation, Hopf bifurcation, Bogdanov-Takens bifurcation and the persistence analysis. In Section 4, numerical simulations are conducted. And in Section 5, an optimal control problem is proposed, which includes two interventions. Some discussions are given in Section 6. The proofs of our main results are given in Section 7.

2 Model formulation

In this section, based on the algicidal characteristics of algicidal bacteria, we have developed an algae-nutrient-algicidal bacteria model that incorporates nutrient input and the algicidal effect of algicidal bacteria. Our model encompasses four nonlinear ordinary differential equations, including the densities of algae $(A)(mg l^{-1} day^{-1})$, nitrogen $(N)(mg l^{-1} day^{-1})$, phosphorus $(P)(mg l^{-1} day^{-1})$, and algicidal bacteria $(F)(mg \ l^{-1} \ day^{-1})$. The model diagram is shown in Figure 1.1. Taking into account the simultaneous introduction of nitrogen and phosphorus nutrients into the water body resulting from sewage discharge and various other factors, we have established the parameter π to measure the proportional distribution of these two elements. Apart from the alterations in nutrient concentration induced by external environmental factors, the release of cellular contents due to the lysis of algal cells by algolytic bacteria will further elevate the concentrations of nitrogen and phosphorus in the water. Therefore, parameters k_1, k_2 are established to quantify the ratio of nitrogen to phosphorus within the cellular contents. The loss of nitrogen and phosphorus nutrients in water is categorized into two distinct components: natural consumption processes and the growth and absorption by algal cells. Therefore, the following two equations are utilized to track the respective concentrations of nitrogen and phosphorus in water:

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$$\frac{dN}{dt} = \underbrace{(1-\pi)q}_{\text{Nitrogen input from different sources}} + \underbrace{k_1\beta FA}_{\text{Derived from algal cell contents}} \\ - \underbrace{\alpha_0 N}_{\text{Natural consumption}} - \underbrace{\mu NA}_{\text{Consumption by algal growth}} , \qquad (2.1a)$$
$$\frac{dP}{dt} = \underbrace{\pi q}_{\text{Phosphorus input from different sources}} + \underbrace{k_2\beta FA}_{\text{Derived from algal cell contents}} \\ - \underbrace{\alpha_1 P}_{\text{A}} - \underbrace{m PA}_{\text{A}} . \qquad (2.1b)$$

Natural consumption Consumption by algal growth

It is widely known that a significant influx of nutrients into the water leads to eutrophication. Nitrogen and phosphorus nutrients serve as limiting factors for the growth and reproduction of algae, and their increased availability is a crucial factor contributing to the formation of harmful algal blooms. Some biological experiments indicate that although nitrogen and phosphorus are both critical for algal growth, reducing phosphorus levels provides more effective algae control than reducing nitrogen levels (Fastner et al. 2016; Schindler 1974). Therefore, when monitoring the growth of algae stimulated by nitrogen and phosphorus, we assign distinct parameters λ_1 , λ_2 to represent the varying absorption efficiencies of these nutrients by algae, respectively. Although algae can proliferate rapidly in a short period, the mortality caused by factors such as natural cell apoptosis cannot be overlooked. Moreover, multiple methods are often employed in algae bloom control, including physical measures like harvesting, which are used as complementary approaches. Considering these two factors, we introduce the parameter α_2 to represent the depletion rate of algal cells. Algicidal bacteria are highly diverse, and different strains demonstrate markedly varying levels of algicidal efficiency. Xuan et al. reported a *Bacillus* sp. strain, named AF-1, that demonstrates an algicidal efficacy of 90% (Xuan et al. 2017). Zhang et al. introduced a new strain of algicidal bacteria, *Pseudomonas f ragi* YB2, which demonstrates a peak algicidal efficiency of 95.02% (Zhang et al. 2024). Furthermore, the algicidal activity exhibits significant variation depending on the bacterial inoculation density and the concentration of Microcystis aeruginosa (Park et al. 2022). Moreover, variations in environmental temperature and PH levels can differentially impact the algicidal efficiency of the bacteria (Lu et al. 2021; Yu et al. 2019). Here, we set the parameter β to represent the algorithm of algolytic bacteria. The population density of algal cells is described by the following nonlinear differential equation:

$$\frac{dA}{dt} = \underbrace{\lambda_1 \mu NA}_{\text{Nitrogen promotes growth}} + \underbrace{\lambda_2 m PA}_{\text{Phosphorus promotes growth}} - \underbrace{\alpha_2 A}_{\text{Algal cell consumption}} - \underbrace{\beta FA}_{\text{Algal lytic bacteria lyse algal cells}} .$$
(2.1c)

The parameter ω represents the input quantity of algolytic bacteria. It is postulated that the algicidal mechanism of algolytic bacteria is indirect, with some species

consuming themselves after secreting algicidal substances. Therefore, we introduce the parameter δ to quantify the self-consumption rate of algolytic bacteria, while the parameter α_3 is designated to represent the natural mortality rate of these bacteria. The following nonlinear differential equation is utilized to track the concentration of algicidal bacteria within aquatic systems:

$$\frac{dF}{dt} = \underbrace{\omega}_{\text{Total input of algaeclytic bacteria}} - \underbrace{\alpha_3 F}_{\text{Natural death of algae-lytic bacteria}} - \underbrace{\delta FA}_{\text{Consumption of algae-lytic bacteria}}$$
(2.1d)

According to the biological considerations, the initial condition of system (2.1) is given as

$$N(0) > 0, P(0) > 0, A(0) > 0, F(0) > 0.$$
 (2.2)

We assume that all parameter values in system (2.1) are positive. By adopting the basic theorems for ordinary differential equations, we easily show that the solution of system (2.1) with (2.2) is existent, non-negative and unique for $t \ge 0$.

3 Model analysis

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In this section, we state the main results of this paper, whose proofs are given in Section 7.

3.1 Algae-free equilibrium and its stability analysis

For system (2.1), there always exists a unique algae-free equilibrium $E_0 = (N_0, P_0, A_0, F_0)$, where $N_0 = \frac{(1-\pi)q}{\alpha_0}$, $P_0 = \frac{\pi q}{\alpha_1}$, $A_0 = 0$, $F_0 = \frac{\omega}{\alpha_3}$. Through the next generation matrix theory (Diekmann et al. 1990; van den Driessche and Watmough 2002), the basic ecological reproductive indices associated with system (2.1) can be defined as

$$R_0 = \frac{\frac{\lambda_1 \mu (1-\pi)q}{\alpha_0} + \frac{\lambda_2 m \pi q}{\alpha_1}}{\alpha_2 + \frac{\beta \omega}{\alpha_3}} = R_1 + R_2,$$

where

$$R_1 = \frac{\lambda_1 \mu (1 - \pi) q}{\alpha_0 \left(\alpha_2 + \frac{\beta \omega}{\alpha_3} \right)}, \ R_2 = \frac{\lambda_2 m \pi q}{\alpha_1 \left(\alpha_2 + \frac{\beta \omega}{\alpha_3} \right)}.$$

The basic ecological reproductive indices R_0 represents the reproductive capacity of algae, and it describes the average number of new algal cells produced by per cubic meter of algae in a aquatic system. The first term R_1 can be interpreted as the contribution to the basic ecological reproductive indices on account of the average number of new algal cells produced by per cubic meter of algae due to the nutrient nitrogen. The second term R_2 can be interpreted as the contribution to the basic ecological reproductive indices on account of the average number of new algal cells produced by per cubic meter of algae due to the nutrient phosphorus.

Theorem 3.1 *The algae-free equilibrium* E_0 *of system* (2.1) *is locally asymptotically stable if* $R_0 < 1$ *and unstable if* $R_0 > 1$.

3.2 Algae-present equilibrium and its stability analysis

For convenience, let us define the parameter

$$\lambda_1^* = \frac{\alpha_0}{\mu(1-\pi)q} \left(\frac{-\lambda_2 m \pi q}{\alpha_1} + \alpha_2 + \frac{\beta \omega}{\alpha_3} \right).$$

From system (2.1), we obtain

$$N = \left[(1 - \pi)q + \frac{k_1\beta\omega A}{\alpha_3 + \delta A} \right] \frac{1}{\alpha_0 + \mu A},$$

$$P = \left(\pi q + \frac{k_2\beta\omega A}{\alpha_3 + \delta A} \right) \frac{1}{\alpha_1 + mA}, \ F = \frac{\omega}{\alpha_3 + \delta A}.$$

After a simple calculation, we obtain

$$\frac{\lambda_1 \mu}{\alpha_0 + \mu A} \left[(1 - \pi)q + \frac{k_1 \beta \omega A}{\alpha_3 + \delta A} \right] + \frac{\lambda_2 m}{\alpha_1 + m A} \left(\pi q + \frac{k_2 \beta \omega A}{\alpha_3 + \delta A} \right) - \alpha_2 - \frac{\omega \beta}{\alpha_3 + \delta A} = 0.$$
(3.1)

Eq. (3.1) can be reduced to

$$G(A) = A^{3} + p_{2}A^{2} + p_{1}A + p_{0} = 0,$$
(3.2)

where

$$p_{0} = -\frac{\alpha_{0}\alpha_{1}\alpha_{3}}{\alpha_{2}\delta m\mu} \left[\frac{\lambda_{1}\mu(1-\pi)q}{\alpha_{0}} + \frac{\lambda_{2}m\pi q}{\alpha_{1}} - \alpha_{2} - \frac{\beta\omega}{\alpha_{3}} \right],$$

$$p_{1} = -\frac{1}{\alpha_{2}\mu\delta m} \left[-\alpha_{0}(\alpha_{1}\alpha_{2}\delta + \alpha_{2}\alpha_{3}m) - \alpha_{1}\beta\mu\omega - \alpha_{1}\alpha_{2}\alpha_{3}\mu - \alpha_{0}\beta m\omega - \alpha_{1}\delta\lambda_{1}\mu(\pi-1)q - \alpha_{3}\lambda_{1}m\mu(\pi-1)q + \alpha_{0}\delta\lambda_{2}m\pi q + \alpha_{3}\lambda_{2}m\mu\pi q + \alpha_{0}\beta k_{2}\lambda_{2}m\omega + \alpha_{1}\beta k_{1}\lambda_{1}\mu\omega \right],$$

$$p_{2} = -\frac{1}{\alpha_{2}\mu\delta m} \left[-\mu(\alpha_{1}\alpha_{2}\delta + \alpha_{2}\alpha_{3}m) - \beta m\mu\omega - \alpha_{0}\alpha_{2}\delta m - \delta\lambda_{1}m\mu q(\pi-1) \right]$$

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 $+\delta\lambda_2m\mu\pi q + \beta k_1\lambda_1m\mu\omega$ $+\beta k_{2}\lambda_{2}m\mu\omega$].

If $p_2^2 \leq 3p_1$, then G(A) is monotonically nondecreasing and it has exactly one real root. If $p_2^2 > 3p_1$, the derivative function $\dot{G}(A) = 3A^2 + 2p_2A + p_1$ has two different real zeros

$$A_{\pm}:\frac{-p_2\pm\sqrt{p_2^2-3p_1}}{3},$$

and G(A) achieves its local maximum at A_{-} and local minimum at A_{+} with

$$G(A_{\pm}) = \frac{-2(p_2^2 - 3p_2)A_{\pm} + 9p_0 - p_1p_2}{9}.$$

In addition, $G(A_{\pm}) \ge 0$ if and only if $A_{\pm} \le \frac{9p_0 - p_1 p_2}{2(p_2^2 - 3p_2)}$. According to (Pan et al. (2019), Lemma 4.2), the number of simple positive zeros of G(A) is discussed in the following theorem.

Theorem 3.2 (H_0) : System (2.1) does not have any algae-present equilibrium if and only if one of the following conditions is satisfied

- p2² ≤ 3p1 and R0 ≤ 1;
 p2² > 3p1, R0 ≤ 1 and A+ ≤ 0;
- $p_2^2 > 3p_1$, $R_0 < 1$ and G(A+) > 0.

(H₁): System (2.1) has a unique algae-present equilibrium if and only if one of the following conditions is satisfied

- $p_2^2 < 3p_1$, and $R_0 > 1$;
- $p_2^2 = 3p_1$, $R_0 > 1$ and $p_2^3 \neq 27p_0$;
- $p_2^2 > 3p_1$, $R_0 > 1$ and $A_- < 0$;
- $p_2^2 > 3p_1$, $R_0 > 1$ and $G(A_-)G(A_+) > 0$;
- $p_2^2 > 3p_1$, $R_0 = 1$ and $A_- < 0 < A_+$.

 (H_2) : System (2.1) has two algae-present equilibria if and only if one of the following conditions is satisfied

- $p_2^2 > 3p_1$, $R_0 < 1$, $A_+ > 0$ and $G(A_+) < 0$;
- $p_2^2 > 3p_1$, $R_0 = 1$, $A_- > 0$ and $G(A_+) < 0$.

(H₃) : System (2.1) has three algae-present equilibria if and only if

• $p_2^2 > 3p_1$, $R_0 > 1$, $A_- > 0$ and $G(A_-)G(A_+) < 0$.

The complete classifications for the existence of simple positive roots of (3.2) are listed in Table 1.

To verify the conclusions of Theorem 3.2, we conducted numerical simulations resulting in Figure 3.1. In Figure 3.1 (a), the curve does not intersect the positive half-axis of A(t), indicating that G(A) = 0 has no positive roots, and thus system (2.1) does not have any algae-present equilibrium. Similarly, Figure 3.1 (b), (c) and (d), depict system (2.1) having 1, 2, and 3 algae-present equilibria, respectively.

Cases	R_0	Parameter conditions	Simple positive roots
1	$R_0 \leq 1$	$p_2^2 \le 3p_1$	0
2	$R_0 \leq 1$	$p_2^2 > 3p_1, A_+ \le 0$	0
3	$R_0 \leq 1$	$p_2^2 > 3p_1, G(A_+) > 0$	0
4	$R_0 > 1$	$p_2^2 < 3p_1$	1
5	$R_0 > 1$	$p_2{}^2 = 3p_1, p_2{}^3 \neq 27p_0$	1
6	$R_0 > 1$	$p_2^2 > 3p_1, A < 0$	1
7	$R_0 > 1$	$p_2^2 > 3p_1, G(A)G(A_+) > 0$	1
8	$R_0 = 1$	$p_2^2 > 3p_1, A \le 0 < A_+$	1
9	$R_0 < 1$	$p_2^2 > 3p_1, A_+ > 0, G(A_+) < 0$	2
10	$R_0 = 1$	$p_2^2 > 3p_1, A > 0, G(A_+) < 0$	2
11	$R_0 > 1$	$p_2^2 > 3p_1, A > 0, G(A)G(A_+) < 0$	3

 Table 1 Classifications of simple positive roots of (3.2)



Fig. 3.1 Possible shapes of the graph of G(A) = 0

Theorem 3.3 Assume that $R_0 > 1$ and the following conditions (i) - (iv) are satisfied. Then algae-present equilibrium $E^* = (N^*, P^*, A^*, F^*)$ of system (2.1) is locally asymptotically stable.

(i)
$$C_i > 0(i = 1, ..., 4),$$

(ii) $C_1C_2 - C_3 > 0,$
(iii) $C_1(C_2C_3 - C_1C_4) - C_3^2 > 0,$
(iv) $C_1(C_2C_3C_4 - C_1C_4^2) - C_3^2C_4 + C_1 > 0,$

where C_i (i = 1, 2, 3, 4) are given in Appendix.

3.3 Backward and forward bifurcations

Theorem 3.4 *The following statements are valid:*

(i) *If*

$$\frac{\lambda_1\mu k_1\beta\omega}{\alpha_0\alpha_3} + \frac{\lambda_2mk_2\beta\omega}{\alpha_1\alpha_3} + \frac{\delta\omega\beta}{\alpha_3^2} > \frac{\lambda_1\mu^2(1-\pi)q}{\alpha_0^2} + \frac{\lambda_2m^2\pi q}{\alpha_1^2},$$

then system (2.1) undergoes a backward bifurcation at $R_0 = 1$; (ii) If

$$\frac{\lambda_1\mu k_1\beta\omega}{\alpha_0\alpha_3} + \frac{\lambda_2mk_2\beta\omega}{\alpha_1\alpha_3} + \frac{\delta\omega\beta}{\alpha_3^2} < \frac{\lambda_1\mu^2(1-\pi)q}{\alpha_0^2} + \frac{\lambda_2m^2\pi q}{\alpha_1^2},$$

then system (2.1) undergoes a forward bifurcation at $R_0 = 1$.

In biology, the existence of backward bifurcation implies that stable algae-free equilibrium and stable algae-present equilibrium may be coexistent. This means that the basic ecological reproductive indices R_0 is not the threshold value, which is used to determine whether algae can be removed successfully or not. In this case, more complicated dynamical behavior may occur. There may exist a new threshold value, which is less than R_0 and used to determine whether algae can be removed successfully or not.

3.4 Transcritical bifurcation and saddle-node bifurcation

Theorem 3.5 System (2.1) undergoes a transcritical bifurcation at $E_0(N_0, P_0, 0, F_0)$ with respect to bifurcation parameter $\lambda_1 = \lambda_1^*$ if

$$\lambda_1 \mu \left(\frac{k_1 \beta \omega}{\alpha_0 \alpha_3} - \frac{\mu (1 - \pi) q}{\alpha_0^2} \right) + \lambda_2 m \left(\frac{k_1 \beta \omega}{\alpha_1 \alpha_3} - \frac{m \pi q}{\alpha_1^2} \right) + \frac{\beta \delta \omega}{\alpha_3^2} \neq 0.$$

Theorem 3.5 shows that an increase in the nitrogen uptake rate by algal cells leads to a transition in the system from an algae-free equilibrium to one supporting algal growth. This indicates that when the nitrogen uptake rate exceeds a critical level, algae can establish themselves in the environment and resist removal.

Theorem 3.6 System (2.1) undergoes a saddle-node bifurcation at $E^*(N^*, P^*, A^*, F^*)$ with respect to bifurcation parameter $\delta = \delta_{SN}^*$ which satisfies

(i) $C_4 = 0$, and $C_3 \neq 0$; (ii) $\frac{\delta_{SN}^* a_2}{a_1} \neq 0$.

According to Theorem 3.6, the consumption rate δ of algicidal bacteria is crucial in a codimension-one saddle-node bifurcation. At the critical value δ_{SN}^* , two algaepresent equilibria merge into a single unique equilibrium E^* . As δ surpasses δ_{SN}^* , transitioning from left to right, the population of algal cells declines, ultimately causing harmful algal blooms to disappear.

3.5 Hopf bifurcation

Theorem 3.7 System (2.1) exhibits a Hopf bifurcation at $E^*(N^*, P^*, A^*, F^*)$ when bifurcation parameter δ passes through the critical value δ_H^* which satisfies

(i) $C_i(\delta_H^*) > 0, i = 1, 2, 3, 4;$ (ii) $C_3(\delta_H^*)[C_1(\delta_H^*)C_2(\delta_H^*) - C_3(\delta_H^*)] - C_1(\delta_H^*)^2 C_4(\delta_H^*) = 0;$ (iii) $\frac{d}{d\delta}[C_1(\delta_H^*)C_2(\delta_H^*)C_3(\delta_H^*) - C_3(\delta_H^*)^2 - C_1(\delta_H^*)^2 C_4(\delta_H^*)] \neq 0.$

Theorem 3.7 emphasizes the pivotal role of the parameter δ in triggering a Hopf bifurcation. Upon reaching its critical threshold δ_H^* , δ induces periodic oscillations near the equilibrium. As δ surpasses δ_H^* and the equilibrium becomes unstable, harmful algal blooms display multiple peaks, with the algal population exhibiting a cyclical pattern of increase and decrease over time.

3.6 Bogdanov-Takens bifurcation

In this subsection, we study the occurrence of codimension 2 Bogdanov-Takens bifurcation. Without loss of generality, we consider the following simper system

$$\frac{dP}{dt} = \pi q + k_2 \beta F A - \alpha_1 P - m P A,$$

$$\frac{dA}{dt} = \lambda_2 m P A - \alpha_2 A - \beta F A,$$

$$\frac{dF}{dt} = \omega - \alpha_3 F - \delta F A.$$
(3.3)

Theorem 3.8 Choosing k_2 and α_1 as two bifurcation parameters, denoting $\psi_1 = k_2 - k_{2BT}$, $\psi_2 = \alpha_1 - \alpha_{1BT}$, system (3.3) undergoes a Bogdanov-Takens bifurcation in a small domain of $(P_{BT}^*, A_{BT}^*, F_{BT}^*)$ as (k_2, α_1) varying near (k_{2BT}, α_{1BT}) if the conditions (BT1)-(BT4) are satisfied. The dynamics on the center manifold of (3.3) is locally topologically equivalent to (3.3). The local representations of the bifurcation curves are given as follows:

(i) The saddle-node bifurcation curve $SN = \{(\psi_1, \psi_2) | 4\bar{\zeta_1} - \bar{\zeta_2}^2 = 0\}$;

(ii) The Hopf bifurcation curve $H = \{(\psi_1, \psi_2) | \bar{\zeta_1} = 0, \bar{\zeta_2} < 0\};$ (iii) The homoclinic bifurcation curve $HL = \{(\psi_1, \psi_2) | \bar{\zeta_1} = -\frac{6}{25} \bar{\zeta_2}^2 + o(\bar{\zeta_2}^2), \bar{\zeta_2} < 0\}.$

Theorem 3.8 indicates the combined impact of the ratio of phosphorus within the cellular contents k_2 and natural consumption rate α_1 in the occurrence of codimension 2 Bogdanov-Takens bifurcation. When (k_2, α_1) attains the critical value (k_{2BT}, α_{1BT}) , algae-present equilibrium becomes a cusp. The changes of parameters k_2 and α_1 in the neighborhood of (k_{2BT}, α_{1BT}) , effect the algal dynamics due to the presence of three different bifurcations including saddle-node bifurcation, Hopf bifurcation and homoclinic bifurcation. Algae may or may not exist on the saddle-node bifurcation curve. Algae blooms occur on the Hopf bifurcation curve. Algae blooms occur on the homoclinic bifurcation curve depending on the initial algae size.

Example 3.9 The codimension 2 bifurcation is verified numerically at the Bogdanov-Takens bifurcation point $(k_2, \alpha_1) = (k_{2BT}, \alpha_{1BT}) = (0.849190, 0.004696)$ when remaining all parameters are fixed at $\alpha_2 = 0.1$, $\alpha_3 = 0.4$, $\pi = 0.1$, q = 0.3, m = 0.5, $\omega = 1$, $\lambda_2 = 1.1$, $\beta = 1.5$, $\delta = 0.1$.

It can be caculated

$$U_0 = (6.3684, 0.0112, 2.4930)^T, \ \rho_0 = (0.8492, 0.0047)^T,$$

$$T_1 = (0, -1.6089, 1.0000)^T, \ T_2 = (-259.2488, -5.6201, 1.0000)^T,$$

$$T_0 = (0, 1.0000, 24.2538)^T,$$

$$Z_1 = (0.0329, -1.5089, 0.0622)^T, \ Z_2 = (-0.0039, 0, 0)^T,$$

$$Z_0 = (-0.0012, 0.0622, 0.0387)^T,$$

$$a = 0.0079 \neq 0, \ b = -8.1670 \neq 0,$$

$$S_1 = (-0.0002, 0.0246)^T, \ S_2 = (0.0238, -0.2538)^T,$$

and

$$S = \begin{pmatrix} -0.0002 & 0.0238\\ 0.0246 & -0.2538 \end{pmatrix}, \ rank(S) = 2.$$

Thus, the conditions (BT1)-(BT4) are satisfied. Furthermore, we assume

$$\begin{cases} \psi_1 = k_2 - 0.849190, \\ \psi_2 = \alpha_1 - 0.004696, \end{cases}$$

then

$$\begin{aligned} \zeta_1 &= S_1^T (\hat{\rho} - \rho_0) = 0.0245658\psi_2 - 0.0001611\psi_1, \\ \zeta_2 &= S_2^T (\hat{\rho} - \rho_0) = 0.0238283\psi_1 - 0.2537931\psi_2. \end{aligned}$$

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(3.4)

Therefore, the dynamics on the center manifold of system (3.3) near (U_0, ρ_0) is topologically equivalent to the following system:

$$\dot{x_1} = x_2,$$

$$\dot{x_2} = 0.0245658\psi_2 - 0.0001611\psi_1 + x_1(0.0238283\psi_1 - 0.2537931\psi_2)$$

$$-8.1669562x_1x_2 + 0.0079057x_1^2.$$

Then a new time \overline{t} and new variables X_1 and X_2 given by

$$t = 1033.0463657\bar{t}, x_1 = 0.000119X_1, x_2 = 0.0000001X_2.$$

System (3.4) can be written as the following form

$$\begin{cases} \dot{X}_1 = X_2, \\ \dot{X}_2 = 221182176.5183669\psi_2 - 1450372.2278895\psi_1 \\ -X_1X_2 + X_1(25429.1489025\psi_1 - 270844.1496669\psi_2) \\ +X_1^2. \end{cases}$$

In addition, $\det\left(\frac{\partial(\bar{\zeta}_1,\bar{\zeta}_2)}{\partial(k_2,\alpha_1)}\right)\Big|_{(k_2,\alpha_1)=(k_{2BT},\alpha_{1BT})} = -5231649668491.9062500 \neq 0$, which ensures the smooth change of the parameters near (k_{2BT}, α_{1BT}) . The local bifurcation curves are as follows:

(i) The saddle-node bifurcation curve

$$SN = \{(\psi_1, \psi_2) | \psi_1^2 - 21.3018651\psi_1\psi_2 + 0.0089717\psi_1 + 113.4423641\psi_2^2 - 1.3681902\psi_2 = 0\};$$

(ii) The Hopf bifurcation curve $H = \{(\psi_1, \psi_2) | \psi_1 = 152.5002839\psi_2, \psi_2 < 0\};$ (iii) The homoclinic bifurcation curve $HL = \{(\psi_1, \psi_2) | \psi_1^2 - 21.301865\psi_1\psi_2 - 0.009346\psi_1 + 113.442364\psi_2^2 + 1.425198\psi_2 = o(|(\psi_1, \psi_2)|^2), \psi_1 - 10.650933\psi_2 < 0\}.$

3.7 Permanence

Theorem 3.10 If $R_0 > 1$, then system (2.1) is permanent. Namely, each positive solution $(N(t), P(t), A(t), F(t))^T$ of system (2.1) with (2.2) satisfies

$$\lim_{t \to \infty} \inf N(t) \ge \frac{(1-\pi)q}{\alpha_0 + \mu\gamma} = \upsilon_1, \lim_{t \to \infty} \inf P(t) \ge \frac{\pi q}{\alpha_1 + m\gamma} = \upsilon_2,$$
$$\lim_{t \to \infty} \inf A(t) \ge \theta_2 e^{-[\alpha_2 + \beta(\frac{\omega}{\alpha_3} + \rho_0)]d} = \upsilon_3, \lim_{t \to \infty} \inf F(t) \ge \frac{\omega}{\alpha_3 + \delta\frac{\omega}{\alpha_3}} = \upsilon_4,$$

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where

$$T_1 = -\frac{1}{\alpha_0 + \mu\theta_2} \ln \frac{\mu(\theta_1 - \theta_2)}{\alpha_0 + \mu\theta_1}, T_2 = -\frac{1}{\alpha_1 + m\theta_2} \ln \frac{m(\theta_1 - \theta_2)}{\alpha_1 + m\theta_1}, d = \max\{T_1, T_2\}.$$

4 Numerical simulations and controlling strategies for algal bloom

In this section, we conduct numerical simulations to illustrate some interesting dynamical phenomena and provide controlling strategies for algal bloom, in which all the parameters are listed in Table 2.

4.1 Sensitivity analysis of R₀

As shown in Figure 4.1, we specify the number of input samples as 10,000 and generate these samples using Latin Hypercube Sampling (LHS) (Marino et al. 2008). The sensitivity of the input parameters is evaluated using the Input/Output Correlation method, which calculates the statistical correlation between the input parameters and basic ecological reproductive indices R_0 . We observe that parameters α_3 , π , q, m and λ_2 have a strong positive influence on R_0 , in which q has the largest positive influence on R_0 . From the numerical point of view, the sensitivity values of parameters μ and λ_1 related to nitrogen absorption by algae are 0.04529 and 0.02599, respectively, while the sensitivity values of parameters π , q, m, λ_2 related to nutrient phosphorus absorption are 0.3633, 0.4293, 0.3851, 0.3605, respectively. In biology, the limiting effect of phosphorus for algal cell reproduction is stronger than that of nitrogen, which aligns with the experimental result in (Luo 2023; Zhang et al. 2024).

To achieve the purpose of controlling the continuous reproduction of algal cells, we need to theoretically reduce the value of R_0 . Observing Figure 4.1, we see that the parameters α_1 , β and ω have opposite effects on the growth of R_0 , with α_1 having the greatest effect. From the biological point of view, reducing the input of nutrient salt phosphorus, selecting algal lytic bacteria with high algal killing rate and appropriately increasing the input of algal lytic bacteria are effective to control algal reproduction. The parameters α_2 and α_0 shown in Figure 4.1, which have little influence on the reduction of R_0 value, also indicate that it is not a reasonable and effective measure to control the development of algal blooms only by the natural death of algae or the control of nutrient nitrogen input.

4.2 Bifurcation analysis

4.2.1 Backward and forward bifurcations

To explore the existence of backward bifurcation for system (2.1), we calculate that a = 452.897 and b = 0.484 by choosing $\lambda_1 = 0.8$. Note that a and b are non-negative, it then follows from Theorem 3.4 that system (2.1) exists a backward bifurcation. Whereafter, we numerically calculate the $R_0 = 0.133 < 1$ and obtain the possible equilibria

Table 2 Parameters of system (2.1) with corresponding values in various figures	
Parameter	Description
0ω	Natural loss rate of nitrogen
α_1	Natural loss rate of phosphorus
α_2	Loss rate of algal cells
α3	Natural loss rate of algicidal bacteria
Д	Fraction of nutrients contributing to the growth of phosphorus
<i>b</i>	Input rate of nutrients
π	Uptake rate of nitrogen by algae
m	Uptake rate of phosphorus by algae
0	Input rate of algicidal bacteria
λ1	Growth of algae due to uptake of nitrogen
λ2	Growth of algae due to uptake of phosphorus
β	Algae lysis rate by algicidal bacteria
8	Consumption rate of algicidal bacteria during the algal lysis process
k1	Nitrogen proportion in intracellular nutrients of lysed algal cells
k2	Phosphorus proportion in intracellular nutrients of lysed algal cells

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Table 2 con	ntinued														
Parameter															Description
Parameter	Figure														Unit
	3.1(a)	3.1(b)	3.1(c)	3.1(d)	4.1	4.2	4.3	4.4(a)	4.4(b)	4.5-4.8	4.9	5.1	5.2(a)	5.2(b)	
α_0	3	2	4	1	4	4	0.4	2	1	0.00465	4	1	1	2	day^{-1}
α_1	0.6	10	7	8	7	7	0.005	10	8	0.1	3	8	8	10	day^{-1}
α_2	10	10	10	10	10	10	0.15	10	10	0.4	10	13	13	10	day^{-1}
α3	8	6	8	20	8	8	0.9	6	20	0.1	8	19	19	6	day^{-1}
π	0.1	0.1	0.1	0.5	0.1	0.1	0.1	0.1	0.9	0.1	0.1	0.9	0.9	0.1	
q	2.15	1.4	2.15	4	4	2.15	0.1	1.4	4	0.3	5	4	4	1.4	$mg \ l^{-1} day^{-1}$
Π	1	10	1.5	26	1	1	0.9	10	20	2	1	18	18	10	$(mg \ l^{-1})^{-1} day^{-1}$
ш	2	10	20	7.9	20	20	0.2	10	7	0.5	20	7	7	10	$(mg \ l^{-1})^{-1} day^{-1}$
3	10	10	10	22.3	10	10	0.3	10	20	1	3	20	20	10	$mg \ l^{-1} day^{-1}$
λ_1	0.8	15	0.8	0.8	0.8	0.8	0.8	ı	0.8	0.8	0.8	0.8	0.8	15	
λ_2	5.3	10	5.3	5.5	5.3	5.3	0.1	10	5.5	1.2	٢	5.5	5.5	10	
β	3	2	14	16	14	14	0.01	2	12	1.5	10	1	1	2	$(mg \ l^{-1})^{-1} day^{-1}$
δ	23	6	23	12	23	23	0.2	6			23	10	10	6	$(mg \ l^{-1})^{-1} day^{-1}$
k_1	0.01	0.02	0.01	0.03	0.01	0.01	0.02	0.02	0.03	0.05	·	0.03	0.03	0.02	
k_2	0.7	0.98	0.7	0.6	0.7	0.7	0.07	0.98	0.6	0.08		0.2	0.2	0.98	ı



Fig. 4.1 Sensitivity analysis of different parameters to R_0

are: (1) $E_0 = (0.484, 0.031, 0, 1.250)$, (2) $E_1^* = (0.421, 0.146, 0.692, 0.418)$, (3) $E_2^* = (0.444, 0.165, 0.430, 0.558)$, respectively. The corresponding eigenvalues of $J_{E_1^*}$ are listed as $-36.616, -3.885 \pm 2.345i, -5.051$, which implies that $J_{E_1^*}$ is a stable equilibrium. The corresponding eigenvalues of $J_{E_2^*}$ are displayed as -29.443, 2.583, -4.376, -6.724, which indicates that $J_{E_2^*}$ is an unstable equilibrium. It is clearly seen from Figure 4.2 that system (2.1) has two stable equilibria for $R_0 < 1$. The solid and black lines represent the stability of E_1^* and E_0 , while dotted curve describes the unstable E_2^* and dotted black curve depicts the unstable E_0 .

The existence of backward bifurcations complicates the control of harmful algal blooms, as reducing R_0 below 1 does not guarantee the elimination of algae. Therefore, we use numerical simulations to evaluate the impact of the parameters λ_2 , k_2 , ω , and β on the phenomenon of backward bifurcation. We set the initial parameter values $\lambda_2 = 5.3, k_2 = 0.7, \omega = 10$, and $\beta = 14$, and observe changes in the backward bifurcation by varying each of these four parameters individually. Figure 4.2 (a) and (b) show the effects of changing λ_2 and k_2 , respectively, while keeping the other parameters constant. It is clear that as λ_2 and k_2 decrease, the bifurcation curve shifts backward to the right, indicating a reduced likelihood of backward bifurcation, which aids in controlling the sustained reproduction of algae. Figure 4.2 (c) and (d) simulate changes in ω and β , with all other parameters hold constant. We observe that as ω and β increase, the likelihood of backward bifurcation increases, which is detrimental to algae control. This suggests that under such conditions, nutrient replenishment within the system becomes dominant, and the threshold $R_0 = 1$ is insufficient to determine whether an algal bloom can be controlled. At this point, a lower threshold is required to assess algae control effectiveness. Furthermore, it is observed that although the expression for R_0 is independent of k_2 , decreasing k_2 reduces the likelihood of



Fig. 4.2 The influence of some parameters λ_2 , k_2 , ω and β on backward bifurcation

backward bifurcation. Thus, we reasonably infer that this lower threshold for algae control may be related to k_2 .

In a manner similar to investigating backward bifurcations, we fix the initial parameter values at $\lambda_2 = 0.1$, $k_2 = 0.07$, $\omega = 0.3$, $\beta = 0.01$ and observe how changes in these parameters affect forward bifurcations. The Figure 4.3 clearly shows that as λ_2 decreases and β and ω increase, the forward bifurcation curve shifts to the right, indicating a gradual reduction in algal populations, which is beneficial for controlling algal blooms. Notably, altering the value of k_2 does not influence the forward bifurcation. This finding is consistent with the fact that, in scenarios where forward bifurcations occurs, $R_0 = 1$ acts as the threshold for algae control, and its expression is unrelated to k_2 .

4.2.2 Transcritical bifurcation and saddle-node bifurcation

Figure 4.4 (a) displays a bifurcation diagram using the nitrogen uptake rate of algal cells as the bifurcation parameter, which supports Theorem 3.5. Specifically, when $\lambda_1 < \lambda_1^*$, an overly low nitrogen absorption rate results in algal extinction, meaning no algae-present equilibrium exists under these conditions. However, when $\lambda_1 > \lambda_1^*$, the algae-free equilibrium E_0 becomes unstable, and algae-present equilibrium appears.



Fig. 4.3 The influence of some parameters λ_2 , k_2 , ω and β on forward bifurcation



Fig. 4.4 Bifurcation diagrams under different bifurcation parameters

This suggests that a higher nitrogen uptake rate by algal cells supports their growth and reproduction, enabling algae to persist in aquatic environments.

Figure 4.4 (b) presents the saddle-node bifurcation diagram around E^* when δ is chosen as the bifurcation parameter. For the algae-present equilibrium E^* , the critical value $\delta = \delta_{SN}^* = 17.808842$ can be calculated. Using the defined parameter values, it follows that $C_4 = 0.00000619 \approx 0$, $C_3 = 189.5792$. The conditions for a saddle-

node bifurcation, as stated in Theorem 3.6, are thus satisfied. Consequently, Figure 4.4 (b) illustrates that as δ increases within a small neighborhood of the critical value $\delta = \delta_{SN}^* = 17.808842$, the number of algae-present equilibrium decreases from two to one, and finally from one to zero, indicating that a saddle-node bifurcation occurs near E^* .

4.2.3 Hopf bifurcation

At E^* , we have $C_3(\delta_H^*)[C_1(\delta_H^*)C_2(\delta_H^*) - C_3(\delta_H^*)] - C_1(\delta_H^*)^2 C_4(\delta_H^*) = 8.6850 \times 10^{-10} \approx 0$ when $\delta = \delta_H^* = 0.54857271$. The characteristic equation at $E^* = (8.8193941, 0.42245707, 0.01351725, 9.3096699)$ becomes

 $\rho^4 + 0.2458584\rho^3 + 0.2737403\rho^2 + 0.06365456\rho + 0.003.840316 = 0.$

It is easy to calculate that $C_1 = 0.2459$, $C_2 = 0.2737$, $C_3 = 0.0637$, $C_4 = 0.0038$, hence $C_i(\delta_H^*) > 0$, i = 1, 2, 3, 4. The corresponding eigenvalues of the characteristic equation are -0.106232, -0.139627, $\pm 0.508830i$. It can be caculated that $\frac{d}{d\delta}[C_1(\delta_H^*)C_2(\delta_H^*)C_3(\delta_H^*) - C_3(\delta_H^*)^2 - C_1(\delta_H^*)^2C_4(\delta_H^*)] = -0.03216215 \neq$ 0, all conditions of Theorem 3.7 as mentioned above are satisfied. Thus, for the value of $\delta = \delta_H^* = 0.54857271$, there exists the Hopf bifurcation at E^* . As δ increases beyond the critical value δ_H^* , the algae-present equilibrium transitions from stable to unstable, and a periodic solution emerges precisely when $\delta = \delta_H^*$. The variation of variable N, P, A, F over time t is depicted in Figure 4.5. Furthermore, Figure 4.6 presents the phase portraits corresponding to Figure 4.5. When the conditions of Theorem 3.7 are not satisfied, a Hopf bifurcation may still occur. We set $\delta = 0.555$ and the other parameters are the same as Figure 4.6, then obtain the Figure 4.7 of N, P, A, F over time t at $E^* = (8.8179, 0.04225, 0.0135, 9.3095)$. Figure 4.8 presents the phase portraits corresponding to Figure 4.7.

4.3 Effects of nutrient supplementation levels in the system

The contents of algal cells include a certain quantity of nitrogen and phosphorus. When algicidal bacteria act upon these cells, they cause the algal cells to rupture, releasing their internal contents into the surrounding environment. This process alters the concentration of nitrogen and phosphorus within the system. To explore how changes in nitrogen and phosphorus levels, resulting from this leakage, affect the efficacy of algae control, we carried out a series of numerical simulation experiments. As illustrated in Figure 4.9, the blue line signifies a lower rate of nutrient supplementation to the system environment from lysed algal cells, while the red line denotes a higher rate. The yellow line represents scenarios with no additional nutrient supplementation. In Figure 4.9 (c), upon stabilization, the lines are ranked from top to bottom as follows: red, blue, and yellow. This ordering suggests that, under an identical algicidal strategy, varying degrees of nutrient supplementation within the system can always stimulate the growth and reproduction of algae. Notably, increased levels of nutrient supplementations.



Fig. 4.5 The solution curves of system (2.1) with the initial value (8.8193941, 0.42245707, 0.01351725, 9.3096699), where $\delta = 0.54857271$

Contrasting Figure 4.9 (a) and (b) reveals differing dynamics: in Figure 4.9 (a), the red line stabilizes above the blue line, indicating greater nutrient supplementation leads to higher algae proliferation. Conversely, in Figure 4.9 (b), the stable positions of these lines are reversed. Comparing these two figures elucidates that algae exhibit a lesser dependency on nitrogen compared to phosphorus for their growth, a finding consistent with biological studies. Moreover, in Figure 4.9 (d), the red line settles below all others, suggesting that more intensive efforts to eliminate algae result in a proportionally higher consumption of algicidal bacteria. This observation, coupled with insights from Figure 4.9 (c), underscores the complex relationship between algicidal efficacy and nutrient management within the system.

5 Control strategies

5.1 Optimal control problem

In what follows, two bounded Lebesgue integrable controls $u_1(t)$ and $u_2(t)$ are introduced into system (2.1):



Fig. 4.6 The phase trajectory of system (2.1) with the initial value (8.8193941, 0.42245707, 0.01351725, 9.3096699), where $\delta = 0.54857271$



Fig. 4.7 The solution curves of system (2.1) with the initial value (8.8179, 0.04225, 0.0135, 9.3095), where $\delta = 0.555$



Fig. 4.8 The phase trajectory of system (2.1) with the initial value (8.8179, 0.04225, 0.0135, 9.3095), where $\delta = 0.555$



Fig. 4.9 The impact of varying levels of nutrient replenishment in the system environment

- $u_1(t)$ indicates improving the algicidal efficiency of algicidal bacteria through methods such as controlling water temperature, adjusting PH levels, and increasing light exposure time, or by choosing strains of algicidal bacteria with higher algicidal efficiencies.
- *u*₂(*t*) indicates enhancing the death rate of algal cells using physical methods like mechanical algae removal, clay flocculation, and ultrasonic treatment.

It is rational to postulate that the control variable pair $u = (u_1, u_2) \in \mathcal{U}$ is Lebesgue measurable, where $\mathcal{U} = \{(u_1, u_2) | 0 \le u_i \le 1, t \in [0, t_f], i = 1, 2\}$ and t_f is the time period of integrated control strategy.

Based on the above hypotheses, one defines that $\beta \rightarrow \beta(1 + u_1(t))$ and $\alpha_2 \rightarrow \alpha_2(1 + u_2(t))$, then system (2.1) with two control measures can be depicted by the following form:

$$\frac{dN}{dt} = (1 - \pi)q + k_1(1 + u_1)\beta FA - \alpha_0 N - \mu NA,$$

$$\frac{dP}{dt} = \pi q + k_2(1 + u_1)\beta FA - \alpha_1 P - m PA,$$

$$\frac{dA}{dt} = \lambda_1 \mu NA + \lambda_2 m PA - (1 + u_2)\alpha_2 A - (1 + u_1)\beta FA,$$

$$\frac{dF}{dt} = \omega - \alpha_3 F - \delta FA.$$
(5.1)

To minimize the cost of microcystis aeruginosa management by implementing two control measures, an objective function

$$J(u) = \int_0^{t_f} \left[A_1 N + A_2 P + A_3 A + \frac{1}{2} B_1(u_1)^2 + \frac{1}{2} B_2(u_2)^2 \right] dt,$$
(5.2)

where A_i (i = 1, 2, 3) stand for the weight of nitrogen and phosphorus nutrients and the number of algae, B_i (i = 1, 2) represent weight coefficients, which indicates the cost per unit of production for different levels of controls. The term

$$\int_0^{t_f} (A_1N + A_2P + A_3A)dt$$

depicts the total number of algae over time t_f . The term

$$\int_0^{t_f} \left(\frac{1}{2} B_1 u_1^2 + \frac{1}{2} B_2 u_2^2 \right) dt$$

shows the total cost of controlling the algae population. Certainly, we try to find out an optimal control $u^* = (u_1^*, u_2^*)$ such that $J(u^*) = \min_{\mathcal{U}} J(u)$.

Theorem 5.1 There exists an optimal control $u^* = (u_1^*, u_2^*)$ such that $J(u^*) = \min_{\mathcal{U}} J(u)$.

We construct the Hamiltonian function from (5.1) and (5.2) to obtain the optimality conditions. Define

$$\begin{aligned} \mathscr{H} &= \left[A_1 N + A_2 P + A_3 A + \sum_{i=1}^2 \frac{1}{2} B_i u_i(t)^2 \right] \\ &+ \xi_1 [(1-\pi)q + k_1 (1+u_1)\beta F A - \alpha_0 N - \mu N A] \\ &+ \xi_2 [\pi q + k_2 (1+u_1)\beta F A - \alpha_1 P - m P A] \\ &+ \xi_3 [\lambda_1 \mu N A + \lambda_2 m P A - \alpha_2 (1+u_2) A - \beta (1+u_1) F A] \\ &+ \xi_4 (\omega - \alpha_3 F - \delta F A), \end{aligned}$$

where ξ_i (*i* = 1, 2, 3, 4) are the adjoint variables and satisfy the following equations

$$\begin{aligned} \frac{d\xi_1}{dt} &= -\frac{\partial \mathscr{H}}{\partial N} = -A_1 + \xi_1(\alpha_0 + \mu A) - \xi_3 \lambda_1 \mu A, \\ \frac{d\xi_2}{dt} &= -\frac{\partial \mathscr{H}}{\partial P} = -A_2 + \xi_2(\alpha_1 + mA) - \xi_3 \lambda_2 m A, \\ \frac{d\xi_3}{dt} &= -\frac{\partial \mathscr{H}}{\partial A} = -\left[A_3 + \xi_1(k_1(1+u_1)\beta F - \mu N) + \xi_2(k_2(1+u_1)\beta F - mP) \right. \\ &\qquad + \xi_3(\lambda_1 \mu N + \lambda_2 m P - \alpha_2(1+u_2) - \beta(1+u_1)F) - \xi_4 \delta F\right], \\ \frac{d\xi_4}{dt} &= -\frac{\partial \mathscr{H}}{\partial F} = -\left[\xi_1 k_1(1+u_1)\beta A + \xi_2 k_2(1+u_1)\beta A - \xi_3 \beta(1+u_1)A \right. \\ &\qquad - \xi_4 \alpha_3 - \xi_4 \delta A\right] \end{aligned}$$

with the transversal conditions $\xi_i(t_f) = 0$ (i = 1, 2, 3, 4). In light of Pontryagin's maximum principle (Pontryagin et al. 1962), $u^* = (u_1^*, u_2^*)$ satisfies the condition

$$\frac{\partial \mathscr{H}}{\partial u_i} = 0, (i = 1, 2).$$

Therefore, the optimal control $u^* = (u_1^*, u_2^*)$ is subjected to

$$u_{1}^{*} = \min\left\{\max\left\{-\frac{1}{B_{1}}(\xi_{1}k_{1}\beta FA + \xi_{2}k_{2}\beta FA - \xi_{3}\beta FA), 0\right\}, u_{1}\max\right\},\$$
$$u_{2}^{*} = \min\left\{\max\left\{\frac{1}{B_{2}}\xi_{3}\alpha_{2}A, 0\right\}, u_{2}\max\right\}.$$

We define $u_{1 \text{ max}}$ as the maximum control level achieved by adjusting environmental conditions and choosing effective algicidal bacteria, and $u_{2 \text{ max}}$ as the highest control level obtainable through changes in physical algae removal techniques.

5.2 Controlling strategies for algal bloom

In this section, we perform numerical simulations for the optimal control problem. The time step is set to 0.01, with an error tolerance of 0.001, and the control terminal time is 20 days. Meanwhile, the initial values are chosen as follows: $(N_0, P_0, A_0, F_0) = (0.12, 0.2, 0.3, 0.2)$. Considering practical factors, the cost of isolating and researching algicidal bacteria is higher than the cost of increasing the natural mortality rate of algae. Therefore, it is reasonable to assume that $B_1 > B_2$, with $B_1 = 20$ and $B_2 = 17$. To minimize the content of nitrogen, phosphorus, and algal density in the system environment, we assume $A_1 = 10$, $A_2 = 13$ and $A_3 = 17$. Moreover, controlling environmental conditions allows us to sustain high levels of algicidal activity in algicidal bacteria, or we can opt for strains that exhibit higher algicidal efficiency. This leads us to set $u_{1max} = 0.8$. While current algae removal methods, like ultrasonic treatment (Ahn et al. 2003), can boost the loss rate of algal cells, they do not provide a lasting resolution to algal bloom problems. Thus, for physical control measures, we set $u_{2max} = 0.4$.

As shown in Figure 5.1 (a), u_1 maintains its maximum control level of 0.52 and gradually decreases to 0 after 17 days, while the maximum control level for u_2 is 0.34. This indicates that under this control strategy, u_1 requires a higher intensity of control. Figure 5.1 (a)-(d) illustrate a gradual increase in control intensity, with u_1 maintaining its maximum control levels of 0.52, 0.75, 0.79, and 0.8, respectively, for durations of 17.36, 18, 18.14, and 18.28 days. It is clear that as the control intensity increases, the maximum control level required for u_1 also rises, and the duration for which it maintains this level gradually extends. In contrast, the duration for which u_2 maintains its maximum control level does not show a significant increase. This comprehensive analysis indicates that u_1 is the key factor in controlling the continuous reproduction of algae.

Given the complexity of algae control processes, to further explore the effectiveness of biological algae control methods, we set $\beta = 0$ to simulate a scenario where algicidal bacteria have no impact on the system. The simulation results are illustrated in Figure 5.2, with different conditions represented as follows: (i) The blue line represents the total number of algal cells without any optimal control measures; (ii) The red line indicates the number of algal cells when optimal control is applied; (iii) The yellow line shows scenarios where neither optimal control measures nor algicidal bacteria are effective; (iv) The green line depicts situations where optimal control is applied but algicidal bacteria remain ineffective. In Figure 5.2 (a), the yellow line stabilizes above the blue line, and the green line stabilizes above the red line. This reveals that the total number of algal cells is consistently lower when algicidal bacteria are effective compared to when they are not, indicating an algicidal dominance in this scenario. Conversely, in Figure 5.2 (b), conditions are opposite to those in Figure 5.2 (a), suggesting that nutrient supplementation plays a dominant role in this case. A comprehensive analysis of Figure 5.2 (a) and (b) demonstrates that the red line remains consistently below the blue line, highlighting a significant reduction in overall algal numbers after implementing control strategies. This outcome underscores the effectiveness of the controls in managing algal populations. This analysis emphasizes



Fig. 5.1 A schematic diagram of the control intensities u_1 and u_2 under control strategies (a)-(d)



Fig. 5.2 Time series of algae (A) with and without control measures

the crucial role of algicidal bacteria in controlling algal growth and highlights the efficacy of the implemented control strategies in achieving better algae management outcomes. This simulation result aligns with the findings reported in the literature (Luo 2023; Zhang et al. 2024).

6 Concluding remarks

Aquatic environments have long been plagued by the problem of harmful algal blooms (HABs). Among the current approaches to managing HABs, methods that leverage microbial activity to control algae have garnered significant attention. Utilizing algicidal bacteria to lyse algal cells and induce their death represents a promising method for controlling HABs. Few studies, however, have developed mathematical models to describe this process. To the best of our knowledge, this paper is the first work to construct a mathematical model to characterize the impact of nitrogen and phosphorus nutrients on algal cell growth based on the algicidal mechanism of the LG3 strain and the reabsorption of algal cell contents post-lysis.

Our mathematical model can exhibit complex dynamical phenomena. Through bifurcation analysis, under specific parameter conditions, the system can exhibit both backward and forward bifurcations. The existence of transcritical and saddle-node bifurcations is demonstrated using Sotomayor's theorem. Furthermore, we derive the conditions for the existence of Hopf bifurcations and establish the transversality conditions. Bogdanov-Takens bifurcation is explored utilizing the methodologies of normal form theory and the center manifold theorem. By applying persistence theory, we derive an explicit formula for the lower bound of harmful algal blooms. To explore the algicidal efficacy of algicidal bacteria, we consider modifying environmental factors or changing physical algae control strategies, which leads us to formulate an optimal control problem.

Through numerical simulations, we investigate how changes in λ_2 , k_2 , ω and β influence backward and forward bifurcations. Our findings show that as ω and β increase, the probability of backward bifurcation rises, suggesting that nutrient supplementation plays a dominant role. There may exist a threshold lower than $R_0 = 1$ that can better predict the effectiveness of algae control under these conditions. In the case of forward bifurcation, our experiments demonstrate that increasing the phosphorus utilization rate by algal cells, boosting the input of algicidal bacteria, and enhancing their algicidal efficiency all aid in algae removal. Furthermore, we simulate transcritical and saddle-node bifurcations using λ_1 and δ as bifurcation parameters. The simulations reveal that increasing λ_1 , which represents the nitrogen utilization rate by algal cells, hinders algae control efforts. On the other hand, when the consumption rate of algicidal bacteria δ surpasses its critical value δ_{SN}^* , harmful algal blooms are eliminated.

To further explore how nutrient supplementation, caused by the lysis of algal cells, affects algae control, we conduct some numerical simulations as illustrated in Figure 4.9. These experiments show that higher levels of nutrient supplementation within the system result in less effective algae control. We also develop an optimal control strategy, which indicates that biological algae control methods are particularly effective for long-term algae management. Ultimately, the simulations generate two scenarios: one where algae control prevails and the other where nutrient supplementation dominates.

Mathematically, analyzing the global stability of the algae-free equilibrium E_0 in case of backward bifurcations poses some challenges. From a practical standpoint, studying the effects of environmental factors like temperature and light on the algicidal

process seems to be more reasonable. Moreover, since the lysis of algal cells by algicidal bacteria involves a time-dependent process, incorporating time delays to more accurately model this phenomenon is an important area. We leave these challenging problems for future investigation.

7 Proofs

The proof of Theorem 3.1 A simple computation yields that the Jacobian matrix of system (2.1) at E_0 is

$$J(E_0) = \begin{pmatrix} -\alpha_0 & 0 & \frac{k_1 \beta \omega}{\alpha_3} - \frac{\mu(1-\pi)q}{\alpha_0} & 0\\ 0 & -\alpha_1 & \frac{k_2 \beta \omega}{\alpha_3} - \frac{m\pi q}{\alpha_1} & 0\\ 0 & 0 & J_3 & 0\\ 0 & 0 & -\frac{\delta \omega}{\alpha_3} & -\alpha_3 \end{pmatrix},$$
(7.1)

where

$$J_3 = \lambda_1 \mu \frac{(1-\pi)q}{\alpha_0} + \lambda_2 m \frac{\pi q}{\alpha_1} - \alpha_2 - \frac{\beta \omega}{\alpha_3}.$$

The corresponding eigenvalues of characteristic equation of $J(E_0)$ are

$$\eta_1 = -\alpha_0, \ \eta_2 = -\alpha_1, \ \eta_3 = -\alpha_3, \ \eta_4 = \lambda_1 \mu \frac{(1-\pi)q}{\alpha_0} + \lambda_2 m \frac{\pi q}{\alpha_1} - \alpha_2 - \frac{\beta \omega}{\alpha_3}$$

If $R_0 < 1$, then $\eta_4 < 0$. Thus, E_0 is locally asymptotically stable and unstable if $R_0 > 1$. The proof is complete.

The proof of Theorem 3.3 The linearizing matrix of system (2.1) at any E^* can be written as

$$J(E^*) = \begin{pmatrix} -\alpha_0 - \mu A^* & 0 & k_1 \beta F^* - \mu N^* & k_1 \beta A^* \\ 0 & -\alpha_1 - m A^* & k_2 \beta F^* - m P^* & k_2 \beta A^* \\ \lambda_1 \mu A^* & \lambda_2 m A^* & \lambda_1 \mu N^* + \lambda_2 m P^* - \alpha_2 - \beta F^* & -\beta A^* \\ 0 & 0 & -\delta F^* & -\alpha_3 - \delta A^* \end{pmatrix}.$$
(7.2)

The characteristic equation of $J(E^*)$ is

$$\rho^4 + C_1 \rho^3 + C_2 \rho^2 + C_3 \rho + C_4 = 0, \qquad (7.3)$$

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where

$$\begin{split} C_{1} = &\alpha_{0} + \alpha_{1} + \alpha_{2} + \alpha_{3} + A^{*}\delta + F^{*}\beta + A^{*}m + A^{*}\mu - N^{*}\lambda_{1}\mu - P^{*}\lambda_{2}m, \\ C_{2} = &\alpha_{0}(\alpha_{1} + \alpha_{2} + \alpha_{3}) + \alpha_{1}\alpha_{2} + \alpha_{1}\alpha_{3} \\ &+ \alpha_{2}\alpha_{3} + A^{*}(\alpha_{0}\delta + \alpha_{1}\delta + \alpha_{2}\delta + \alpha_{0}m + \alpha_{2}m + \alpha_{3}m + \alpha_{1}\mu + \alpha_{2}\mu + \alpha_{3}\mu) \\ &+ F^{*}(\alpha_{0}\beta + \alpha_{1}\beta + \alpha_{3}\beta) + A^{*2}(\delta m + \delta \mu + m\mu) \\ &+ N^{*}(-\alpha_{0}\lambda_{1}\mu - \alpha_{1}\lambda_{1}\mu - \alpha_{3}\lambda_{1}\mu) + P^{*}(-\alpha_{0}\lambda_{2}m - \alpha_{1}\lambda_{2}m \\ &- \alpha_{3}\lambda_{2}m) + A^{*}N^{*}(-\delta\lambda_{1}\mu - \lambda_{1}m\mu) + A^{*}P^{*}(-\delta\lambda_{2}m - \lambda_{2}m\mu) \\ &+ A^{*}F^{*}(-\beta k_{2}\lambda_{2}m - \beta k_{1}\lambda_{1}\mu + \beta m + \beta \mu), \\ C_{3} = &\alpha_{0}\alpha_{1}\alpha_{2} + \alpha_{0}\alpha_{1}\alpha_{3} + \alpha_{0}\alpha_{2}\alpha_{3} + \alpha_{1}\alpha_{2}\alpha_{3} \\ &+ A^{*2}(\alpha_{0}\delta m + \alpha_{2}\delta m + \alpha_{1}\delta\mu + \alpha_{2}\delta\mu + \alpha_{2}m\mu + \alpha_{3}m\mu + \beta m\mu) \\ &+ A^{*3}\delta m\mu + A^{*}(\alpha_{0}\alpha_{1}\delta + \alpha_{0}\alpha_{2}\delta + \alpha_{1}\alpha_{2}\delta + \alpha_{0}\alpha_{2}m + \alpha_{0}\alpha_{3}m \\ &+ \alpha_{2}\alpha_{3}m + \alpha_{1}\alpha_{2}\mu + alpha_{1}\alpha_{3}\mu + \alpha_{2}\alpha_{3}\mu) \\ &+ F^{*}(\alpha_{0}\alpha_{1}\beta + \alpha_{0}\alpha_{3}\beta + \alpha_{1}\alpha_{3}\beta) + N^{*}(-\alpha_{0}\alpha_{1}\lambda_{1}\mu - \alpha_{1}\alpha_{3}\lambda_{1}\mu) \\ &+ P^{*}(-\alpha_{0}\alpha_{1}\lambda_{2}m - \alpha_{0}\alpha_{3}\lambda_{2}m \\ &- \alpha_{1}\alpha_{3}\lambda_{2}m) + A^{*}F^{*}(\alpha_{3}\beta m + \alpha_{1}\beta\mu + \alpha_{3}\beta\mu - \alpha_{0}\beta k_{2}\lambda_{2}m \\ &- \alpha_{3}\beta k_{2}\lambda_{2}m - \alpha_{1}\beta k_{1}\lambda_{1}\mu - \alpha_{3}\lambda_{1}m\mu) \\ &+ A^{*}P^{*}(-\alpha_{0}\delta\lambda_{1}\mu - \alpha_{1}\delta\lambda_{1}\mu - \alpha_{1}\lambda_{2}m\mu - \alpha_{3}\lambda_{2}m\mu) \\ &- A^{*2}N^{*}\delta\lambda_{1}m\mu - A^{*2}P^{*}\delta\lambda_{2}m\mu + A^{*2}F^{*}(-\beta k_{1}\lambda_{1}m\mu - \beta k_{2}\lambda_{2}m\mu), \\ C_{4} = &\alpha_{0}\alpha_{1}\alpha_{2}\alpha_{3} + A^{*}(\alpha_{0}\alpha_{1}\alpha_{2}\delta + \alpha_{0}\alpha_{2}\alpha_{3}m + \alpha_{1}\alpha_{2}\alpha_{3}\mu) \\ &+ F^{*}\alpha_{0}\alpha_{1}\alpha_{3}\beta + A^{*2}(\alpha_{0}\alpha_{3}\beta m + \alpha_{1}\alpha_{3}\beta\mu - \alpha_{0}\alpha_{3}\beta k_{2}\lambda_{2}m \\ &- \alpha_{1}\alpha_{3}\beta k_{1}\lambda_{1}\mu) - N^{*}\alpha_{0}\alpha_{1}\alpha_{3}\lambda_{1}\mu - P^{*}\alpha_{0}\alpha_{1}\alpha_{3}\lambda_{2}m \\ &- \alpha^{*2}N^{*}\alpha_{0}\delta\lambda_{1}m\mu - A^{*2}P^{*}\alpha_{1}\delta\lambda_{2}m\mu + A^{*N}(-\alpha_{0}\alpha_{1}\delta\lambda_{1}\mu - \alpha_{0}\alpha_{3}\lambda_{1}m\mu) \\ &+ A^{*P}(-\alpha_{0}\alpha_{1}\delta\lambda_{2}m - \alpha_{1}\alpha_{3}\lambda_{2}m) \\ &+ A^{*2}F^{*}(-\alpha_{0}\alpha_{1}\delta\lambda_{1}m - \alpha_{1}\alpha_{3}\lambda_{2}m\mu) \\ &+ A^{*2}F^{*}(-\alpha_{0}\alpha_{1}\delta\lambda_{1}m - \alpha_{1}\alpha_{3}\beta\mu\mu). \end{aligned}$$

On the basis of the Routh-Hurwitz criterion, all roots of (7.3) have negative real parts when the determinants $|M_i|$ (i = 1, ..., 4) are all positive, where

$$M_1 = (C_1), \ M_2 = \begin{pmatrix} C_1 & 1 \\ C_3 & C_2 \end{pmatrix}, \ M_3 = \begin{pmatrix} C_1 & 1 & 0 \\ C_3 & C_2 & C_1 \\ 0 & C_4 & C_3 \end{pmatrix}, \ M_4 = \begin{pmatrix} C_1 & 1 & 0 & 0 \\ C_3 & C_2 & C_1 & 1 \\ 0 & C_4 & C_3 & C_2 \\ 0 & 0 & 0 & C_4 \end{pmatrix}.$$

Therefore, condition (i) means that $|M_1|$ is positive; condition (ii) can make sure that $|M_2|$ is positive; condition (iii) ensures that $|M_3|$ also is positive; and condition (iv) pledges that $|M_4|$ is positive. The proof is complete.

The proof of Theorem 3.4 Without loss of generality, we introduce the new variables $x_1 = N$, $x_2 = P$, $x_3 = A$, $x_4 = F$. System (2.1) is rewritten as the following form:

$$f_{1} = (1 - \pi)q + k_{1}\beta x_{3}x_{4} - \alpha_{0}x_{1} - \mu x_{1}x_{3},$$

$$f_{2} = \pi q + k_{2}\beta x_{3}x_{4} - \alpha_{1}x_{2} - mx_{2}x_{3},$$

$$f_{3} = \lambda_{1}\mu x_{1}x_{3} + \lambda_{2}mx_{2}x_{3} - \alpha_{2}x_{3} - \beta x_{3}x_{4},$$

$$f_{4} = \omega - \alpha_{3}x_{4} - \delta x_{3}x_{4}.$$
(7.4)

Note that at $R_0 = 1$, we have $\lambda_1 = \lambda_1^* = \frac{\alpha_0}{\mu(1-\pi)q} \left(\frac{-\lambda_2 m \pi q}{\alpha_1} + \alpha_2 + \frac{\beta \omega}{\alpha_3} \right)$. The linearized matrix corresponding to system (7.4) around E_0 at $R_0 = 1$ is

$$J(E_0, \lambda_1^*) = \begin{pmatrix} -\alpha_0 & 0 & \frac{k_1 \beta \omega}{\alpha_3} - \frac{\mu(1-\pi)q}{\alpha_0} & 0\\ 0 & -\alpha_1 & \frac{k_2 \beta \omega}{\alpha_3} - \frac{m\pi q}{\alpha_1} & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & -\frac{\delta \omega}{\alpha_3} & -\alpha_3 \end{pmatrix},$$
(7.5)

matrix (7.5) has a simple eigenvalue zero and all other eigenvalues are negative at $R_0 = 1$.

Let $\bar{\omega} = (\omega_1, \omega_2, \omega_3, \omega_4)^T$ be a right eigenvector of the zero eigenvalue at (E_0, λ_1^*) , thus

$$\omega_1 = \frac{1}{\alpha_0} \left[\frac{k_1 \beta \omega}{\alpha_3} - \frac{\mu (1 - \pi) q}{\alpha_0} \right], \ \omega_2 = \frac{1}{\alpha_1} \left(\frac{k_2 \beta \omega}{\alpha_3} - \frac{m \pi q}{\alpha_1} \right), \ \omega_3 = 1, \ \omega_4 = -\frac{\delta \omega}{\alpha_3^2}.$$

Similarly, from the matrix $J(E_0, \lambda_1^*)$, we obtain a left eigenvector $\bar{v} = (v_1, v_2, v_3, v_4)$ (associated with the zero eigenvalue) with components as

 $v_1 = 0, v_2 = 0, v_3 = 1, v_4 = 0.$

Now, we compute the following quantities

$$a = \sum_{k,i,j=1}^{4} v_k \omega_i \omega_j \frac{\partial^2 f_k}{\partial x_i \partial x_j} (E_0, \lambda_1^*), \ b = \sum_{k,i=1}^{4} v_k \omega_i \frac{\partial^2 f_k}{\partial x_i \partial \lambda_1} (E_0, \lambda_1^*),$$

to get

$$a = 2\left[\frac{\lambda_1\mu k_1\beta\omega}{\alpha_0\alpha_3} + \frac{\lambda_2mk_2\beta\omega}{\alpha_1\alpha_3} + \frac{\delta\omega\beta}{\alpha_3^2}\right] - 2\left[\frac{\lambda_1\mu^2(1-\pi)q}{\alpha_0^2} + \frac{\lambda_2m^2\pi q}{\alpha_1^2}\right],$$

$$b = \frac{\mu(1-\pi)q}{\alpha_0} > 0.$$

By (Castillo-Chavez and Song (2004), Theorem 4.1, p.373, and Remark 1, p.375), we obtain the result. The proof is complete.

The proof of Theorem 3.5 According to the Jacobian matrix (7.1), we can easily know that $\eta_{1,2,3} < 0$. When $\lambda_1 = \lambda_1^*$, there exists a unique zero eigenvalue: $\eta_4 = 0$. Let *V*, *W* be the eigenvectors corresponding to the zero eigenvalue of $J(E_0)$ and $J(E_0)^T$ respectively, namely:

$$V = \begin{pmatrix} v_1 \\ v_2 \\ v_3 \\ v_4 \end{pmatrix} = \begin{pmatrix} \frac{k_1 \beta \omega}{\alpha_3 \alpha_0} - \frac{\mu (1 - \pi) q}{\alpha_0^2} \\ \frac{k_2 \beta \omega}{\alpha_3 \alpha_1} - \frac{m \pi q}{\alpha_1^2} \\ 1 \\ -\frac{\delta \omega}{\alpha_3^2} \end{pmatrix}, W = \begin{pmatrix} w_1 \\ w_2 \\ w_3 \\ w_4 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \end{pmatrix}.$$

By using straightfrward calculations, we get

$$F_{\lambda_{1}}(E_{0};\lambda_{1}^{*}) = \begin{pmatrix} 0\\0\\0\\0 \end{pmatrix}, DF_{\lambda_{1}}(E_{0};\lambda_{1}^{*})V = \begin{pmatrix} 0\\0\\\frac{\mu(1-\pi)q}{\alpha_{0}}\\0 \end{pmatrix},$$
$$D^{2}F(E_{0};\lambda_{1}^{*})(V,V) = \begin{pmatrix} -2\mu\left(\frac{k_{1}\beta\omega}{\alpha_{3}\alpha_{0}} - \frac{\mu(1-\pi)q}{\alpha_{0}^{2}}\right) - \frac{2k_{1}\beta\delta\omega}{\alpha_{3}^{2}}\\ -2m\left(\frac{k_{2}\beta\omega}{\alpha_{1}\alpha_{3}} - \frac{m\pi q}{\alpha_{1}^{2}}\right) - \frac{2k_{2}\beta\delta\omega}{\alpha_{3}^{2}}\\ 2\lambda_{1}\mu\left(\frac{k_{1}\beta\omega}{\alpha_{0}\alpha_{3}} - \frac{\mu(1-\pi)q}{\alpha_{0}^{2}}\right) + 2\lambda_{2}m\left(\frac{k_{1}\beta\omega}{\alpha_{1}\alpha_{3}} - \frac{m\pi q}{\alpha_{1}^{2}}\right) + \frac{2\beta\delta\omega}{\alpha_{3}^{2}} \end{pmatrix}.$$

From the above calculation, we obtain as follows:

$$W^{T} F_{\lambda_{1}}(E_{0}; \lambda_{1}^{*}) = 0,$$

$$W^{T} D F_{\lambda_{1}}(E_{0}; \lambda_{1}^{*}) V = \frac{\mu(1-\pi)q}{\alpha_{0}} \neq 0,$$

$$W^{T} D^{2} F(E_{0}; \lambda_{1}^{*}) (V, V) = 2\lambda_{1}^{*} \mu \left(\frac{k_{1}\beta\omega}{\alpha_{0}\alpha_{3}} - \frac{\mu(1-\pi)q}{\alpha_{0}^{2}}\right)$$

$$+ 2\lambda_{2} m \left(\frac{k_{1}\beta\omega}{\alpha_{1}\alpha_{3}} - \frac{m\pi q}{\alpha_{1}^{2}}\right) + \frac{2\beta\delta\omega}{\alpha_{3}^{2}}.$$

If $W^T D^2 F(E_0; \lambda_1^*)(V, V) \neq 0$, i.e., $2\lambda_1^* \mu \left(\frac{k_1 \beta \omega}{\alpha_0 \alpha_3} - \frac{\mu(1-\pi)q}{\alpha_0^2}\right) + 2\lambda_2 m \left(\frac{k_1 \beta \omega}{\alpha_1 \alpha_3} - \frac{m\pi q}{\alpha_1^2}\right) + \frac{2\beta \delta \omega}{\alpha_3^2} \neq 0$, then from Sotomayor's theorem (Perko 2013), system (2.1) undergoes a transcritical bifurcation around E_0 when $\lambda_1 = \lambda_1^*$. The proof is complete.

The proof of Theorem 3.6 From Jacobian matrix (7.2), when $C_4 = 0$ and $C_3 \neq 0$, we get the following equation

$$\rho^4 + C_1 \rho^3 + C_2 \rho^2 + C_3 \rho = 0,$$

then there exists a unique zero eigenvalue $\rho_1 = 0$ and $\rho_{2,3,4} \neq 0$ if $\delta = \delta_{SN}^*$.

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By using Sotomoyor's theorem (Perko 2013), we obtain

$$V = \begin{pmatrix} v_{SN1} \\ v_{SN2} \\ v_{SN3} \\ v_{SN4} \end{pmatrix}, W = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 1 \end{pmatrix},$$

where $v_{SN1} = \frac{\frac{-a_2a_3}{a_1} + k_2\beta A^*}{\alpha + mA^*}$, $v_{SN2} = \frac{\frac{-a_2a_4}{a_1} + k_1\beta A^*}{\alpha_0 + \mu A^*}$, $v_{SN3} = -\frac{a_2}{a_1}$, $v_{SN4} = 1$, and

$$a_{1} = \frac{k_{1}\beta F^{*} - \mu N^{*}}{\alpha_{0} + \mu A^{*}} \lambda_{1}\mu A^{*} + \frac{k_{2}\beta F^{*} - mP^{*}}{\alpha_{1} + mA^{*}} \lambda_{2}mA^{*},$$

$$a_{2} = -\beta A^{*} + \frac{k_{1}\beta A^{*}}{\alpha_{0} + \mu A^{*}} \lambda_{1}\mu A^{*} + \frac{k_{2}\beta A^{*}}{\alpha_{1} + mA^{*}} \lambda_{2}mA^{*}.$$

Then

$$F_{\delta}(E^*; \delta_{SN}^*) = \begin{pmatrix} 0\\ 0\\ 0\\ -F^*A^* \end{pmatrix}, D^2 F_{\delta}(E^*; \delta_{SN}^*)(V, V)$$
$$= \begin{pmatrix} 2k_1 \beta v_{SN3} v_{SN4} - 2\mu v_{SN1} v_{SN3}\\ 2k_2 \beta v_{SN3} v_{SN4} - 2m v_{SN2} v_{SN3}\\ 2\lambda_1 \mu v_{SN1} v_{SN3} + 2\lambda_2 m v_{SN2} v_{SN3} - 2\beta v_{SN3} v_{SN4}\\ -2\delta_{SN}^* v_{SN3} v_{SN4} \end{pmatrix}.$$

A simple computation yields

$$W^{T} F_{\delta}(E^{*}; \delta_{SN}^{*}) = -F^{*}A^{*} \neq 0, \ W^{T}[D^{2}F_{\delta}(E^{*}; \delta_{SN}^{*})(V, V)]$$

= $-2\delta_{SN}^{*}v_{SN3}v_{SN4} = \frac{2\delta_{SN}^{*}a_{2}}{a_{1}}.$

If $\frac{\delta_{SN}^* a_2}{a_1} \neq 0$, then from Sotomayor's theorem, system (2.1) undergoes a saddle-node bifurcation around E^* when $\delta = \delta_{SN}^*$. The proof is complete.

The proof of Theorem 3.7 The Jacobian matrix at E^* is (7.2) and the characteristic equation is

$$\rho^4 + C_1(\delta)\rho^3 + C_2(\delta)\rho^2 + C_3(\delta)\rho + C_4(\delta) = 0.$$
(7.6)

If $\delta = \delta_H^*$ satisfies

$$C_3(\delta_H^*)[C_1(\delta_H^*)C_2(\delta_H^*) - C_3(\delta_H^*)] - C_1(\delta_H^*)^2 C_4(\delta_H^*) = 0.$$
(7.7)

Then

$$C_2(\delta_H^*) = \frac{C_1(\delta_H^*)^2 C_4(\delta_H^*) + C_3(\delta_H^*)^2}{C_1(\delta_H^*) C_3(\delta_H^*)}.$$
(7.8)

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Substitute (7.8) into Eq. (7.6)

$$\left(\rho^{2} + \frac{C_{3}}{C_{1}}\right)\left(\rho^{2} + C_{1}\rho + \frac{C_{1}C_{4}}{C_{3}}\right) = 0.$$
(7.9)

It is evident that Eq. (7.9) has two purely imaginary roots $\rho_{1,2} = \pm w_0 i$, where $w_0 = \sqrt{\frac{C_3}{C_1}}$. For the quadratic equation in ρ , let its roots be denoted by ρ_3 , ρ_4 , which satisfy the following equalities:

$$\rho_3 + \rho_4 = -C_1, \tag{7.10}$$

$$w_0^2 + \rho_3 \rho_4 = C_2, \tag{7.11}$$

$$w_0{}^2(\rho_3 + \rho_4) = -C_3, \tag{7.12}$$

$$w_0{}^2\rho_3\rho_4 = C_4. (7.13)$$

If ρ_3 , ρ_4 are conjugate complex roots, then from Eq. (7.10), it can be computed that $2Re(\rho_3) = -C_1$, indicating that both ρ_3 , ρ_4 have negative real parts. If ρ_3 , ρ_4 are real roots, from Eqs. (7.10)-(7.13), it can be inferred that ρ_3 , ρ_4 are negative numbers. Therefore, all four roots of the characteristic equation (7.6) lie in the left half of the complex plane.

The transversal conditions for generating Hopf bifurcation are further discussed. For any $\delta \in (\delta_H^* - \varepsilon, \delta_H^* + \varepsilon)$, let $\rho_{1,2} = \alpha(\delta) \pm i\beta(\delta)$ be obtained by inserting (7.6) and separating the real and imaginary parts

$$\alpha^{4} + C_{1}\alpha^{3} + C_{2}\alpha^{2} + C_{3}\alpha + C_{4} + \beta^{4} - 6\alpha^{2}\beta^{2} - 3C_{1}\alpha\beta^{2} - C_{2}\beta^{2} = 0,$$

$$4\alpha\beta(\alpha^{2} - \beta^{2}) - C_{1}\beta^{3} + 3C_{1}\alpha^{2}\beta + 2C_{2}\alpha\beta + C_{3}\beta = 0.$$
(7.14)

Since $\beta(\delta) \neq 0$, we obtain

$$-(4\alpha + C_1)\beta^2 + 4\alpha^3 + 3C_1\alpha^2 + 2C_2\alpha + C_3 = 0,$$

then

$$\beta^2 = \frac{4\alpha^3 + 3C_1\alpha^2 + 2C_2\alpha + C_3}{4\alpha + C_1},$$
(7.15)

substituting Eq. (7.15) into Eq. (7.14) gives

$$- 64\alpha^{6} - 96C_{1}\alpha^{5} - 16(3C_{1}^{2} + 2C_{2})\alpha^{4} - (C_{3}(C_{1}C_{2} - C_{3}))$$
$$- C_{1}^{2}C_{4} - 8(C_{1}^{3} + 4C_{1}C_{2})\alpha^{3}$$
$$- 4(C_{2}^{2} + 2C_{1}^{2}C_{2} + C_{1}C_{3} - 4C_{4})\alpha^{2} - 2C_{1}(C_{1}C_{3} + C_{2}^{2} - 4C_{4})\alpha = 0.$$

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Noting that $\alpha(\delta_H^*) = 0$ and $C_4(\delta_H^*) = \frac{C_1(\delta_H^*)C_2(\delta_H^*)C_3(\delta_H^*)-C_3(\delta_H^*)^2}{C_1(\delta_H^*)^2}$ is obtained from (7.7), the differential of the above equation with respect to δ is sorted out

$$\begin{split} \left[\frac{d\alpha}{d\delta}\right]_{\delta=\delta_{H}^{*}} &= \left[\frac{\frac{d}{d\delta}(C_{1}C_{2}C_{3}-C_{3}^{2}-C_{1}^{2}C_{4})}{-2C_{1}(C_{1}C_{3}+C_{2}^{2}-4C_{4})}\right]_{\delta=\delta_{H}^{*}} \\ &= \left[\frac{\frac{d}{d\delta}(C_{1}C_{2}C_{3}-C_{3}^{2}-C_{1}^{2}C_{4})}{-2C_{1}\left[C_{1}C_{3}+C_{2}^{2}-2\left(\frac{2C_{3}}{C_{1}}\right)C_{2}+\left(\frac{2C_{3}}{C_{1}}\right)^{2}\right]}\right]_{\delta=\delta_{H}^{*}} \\ &= \left[\frac{\frac{d}{d\delta}(C_{1}C_{2}C_{3}-C_{3}^{2}-C_{1}^{2}C_{4})}{-2C_{1}\left[C_{1}C_{3}+\left(2\frac{C_{3}}{C_{1}}-C_{2}\right)^{2}\right]}\right]_{\delta=\delta_{H}^{*}}. \end{split}$$

If $\left[\frac{d\alpha}{d\delta}\right]_{\delta=\delta_{H}^{*}} \neq 0$, then we get $\left[\frac{d}{d\delta}(C_{1}C_{2}C_{3}-C_{3}^{2}-C_{1}^{2}C_{4})\right]_{\delta=\delta_{H}^{*}} \neq 0$, which is the transversal condition for generating Hopf bifurcation. The proof is complete.

The proof of Theorem 3.8 First, the Jacobian matrix at $E_{BT}^*(P_{BT}^*, A_{BT}^*, F_{BT}^*)$ is

$$J(E_{BT}^{*}) = \begin{pmatrix} -\alpha_1 - mA_{BT}^{*} & k_2\beta F_{BT}^{*} - mP_{BT}^{*} & k_2\beta A_{BT}^{*} \\ \lambda_2 mA_{BT}^{*} & \lambda_2 mP_{BT}^{*} - \alpha_2 - \beta F_{BT}^{*} & -\beta A_{BT}^{*} \\ 0 & -\delta F_{BT}^{*} & -\alpha_3 - \delta A_{BT}^{*} \end{pmatrix},$$

we get the following equation

$$\chi^3 + C_{BT2}\chi^2 + C_{BT1}\chi + C_{BT0} = 0$$

where

$$C_{BT2} = \frac{\omega}{F_{BT}^{*}} + \alpha_{1} + mA_{BT}^{*} > 0,$$

$$C_{BT1} = -\delta\beta A_{BT}^{*}F_{BT}^{*} + \frac{\alpha_{1}\omega}{F_{BT}^{*}} + \frac{m\omega A_{BT}^{*}}{F_{BT}^{*}} + \lambda_{2}m^{2}A_{BT}^{*}P_{BT}^{*} - \lambda_{2}mk_{2}\beta F_{BT}^{*}A_{BT}^{*},$$

$$C_{BT0} = -\alpha_{1}\delta\beta A_{BT}^{*}F_{BT}^{*} - m\delta\beta A_{BT}^{*2}F_{BT}^{*} + \frac{\lambda_{2}m^{2}\omega A_{BT}^{*}P_{BT}^{*}}{F_{BT}^{*}} - \lambda_{2}mk_{2}\omega\beta A_{BT}^{*} + \lambda_{2}mk_{2}\delta\beta A_{BT}^{*2}F_{BT}^{*}.$$

Then we have a zero eigenvalue of multiplicity 2 if $C_{BT2} \neq 0$, $C_{BT1} = 0$ and $C_{BT0} = 0$. The eigenvalues are $\chi_1 = 0$, $\chi_2 = 0$ and $\chi_3 = -C_{BT2} \neq 0$.

For the sake of argument, let *B* replace the Jacobian matrix of E_{BT}^* when $(k_2, \alpha_1) = (k_{2BT}, \alpha_{1BT})$. The conditions of Bogdanov-Takens bifurcation around $E_{BT}^*(P_{BT}^*, A_{BT}^*, F_{BT}^*)$ will be considered in the following discussions.

System (2.1) is rewritten in a matrix form as

$$\dot{U} = F(U, \hat{\rho})$$

where

$$U = \begin{pmatrix} P \\ A \\ F \end{pmatrix}, \quad \hat{\rho} = \begin{pmatrix} k_2 \\ \alpha_1 \end{pmatrix}, \quad F(U, \hat{\rho}) \triangleq \begin{pmatrix} F_1 \\ F_2 \\ F_3 \end{pmatrix} = \begin{pmatrix} \pi q + k_2 \beta F A - \alpha_1 P - m P A \\ \lambda_2 m P A - \alpha_2 A - \beta F A \\ \omega - \alpha_3 F - \delta F A \end{pmatrix}.$$

Let

$$U_0 = \begin{pmatrix} P_{BT}^* \\ A_{BT}^* \\ F_{BT}^* \end{pmatrix}, \quad \rho_0 = \begin{pmatrix} k_{2BT} \\ \alpha_{1BT} \end{pmatrix},$$

then consider the Taylor series around (U_0, ρ_0) :

$$F(U, \hat{\rho}) = DF(U_0, \rho_0)(U - U_0) + F_{\hat{\rho}}(U_0, \rho_0)(\hat{\rho} - \rho_0) + \frac{1}{2}D^2F(U_0, \rho_0)(U - U_0, U - U_0) + F_{\hat{\rho}U}(U_0, \rho_0)(U - U_0, \hat{\rho} - \rho_0) + \cdots,$$

where

$$B = DF(U_0, \rho_0) = \begin{pmatrix} -\alpha_{1BT} - mA_{BT}^* & k_{2BT}\beta F_{BT}^* - mP_{BT}^* & k_{2BT}\beta A_{BT}^* \\ \lambda_2 m A_{BT}^* & \lambda_2 m P_{BT}^* - \alpha_2 - \beta F_{BT}^* & -\beta A_{BT}^* \\ 0 & -\delta F_{BT}^* & -\alpha_3 - \delta A_{BT}^* \end{pmatrix},$$

$$F_{\hat{\rho}}(U_0, \rho_0) = \begin{pmatrix} \beta F_{BT}^* A_{BT}^* - P_{BT}^* \\ 0 & 0 \\ 0 & 0 \end{pmatrix}.$$

Denote $D^2 F(U_0, \rho_0) = \{D^2 F_1, D^2 F_2, D^2 F_3\}, F_{\hat{\rho}U}(U_0, \rho_0) = \{F_{1\hat{\rho}U}, F_{2\hat{\rho}U}, F_{3\hat{\rho}U}\}$, where

$$D^{2}F_{1} = \begin{pmatrix} 0 & -m & 0 \\ -m & 0 & k_{2BT}\beta \\ 0 & k_{2BT}\beta & 0 \end{pmatrix}, \quad D^{2}F_{2} = \begin{pmatrix} 0 & \lambda_{2}m & 0 \\ \lambda_{2}m & 0 & -\beta \\ 0 & -\beta & 0 \end{pmatrix}, \quad D^{2}F_{3} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & -\delta \\ 0 & -\delta & 0 \end{pmatrix},$$
$$F_{1\hat{\rho}U} = \begin{pmatrix} 0 & \beta F_{BT}^{*} & \beta A_{BT}^{*} \\ -1 & 0 & 0 \end{pmatrix}, \quad F_{2\hat{\rho}U} = F_{3\hat{\rho}U} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

Let T_1 , T_2 be generalized eigenvectors of *B* corresponding to the eigenvalue $\chi = 0$: $BT_1 = 0$ and $BT_2 = T_1$.

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Then we get

$$T_1 = \begin{pmatrix} 0\\ -\frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*}\\ 1 \end{pmatrix}, \quad T_2 = \begin{pmatrix} \frac{\beta}{\lambda_{2m}} - \frac{\alpha_3 + \delta A_{BT}^*}{\delta \lambda_{2m} F_{BT}^* A_{BT}^*}\\ -\frac{\alpha_3 + \delta A_{BT}^* + 1}{\delta F_{BT}^*}\\ 1 \end{pmatrix}.$$

Let $T = (T_1, T_2, T_0)$, where T_0 contains the generalized eigenvectors of (χ_3) which is a 1×1 matrix. It is known that

$$T_0 = \begin{pmatrix} 0 \\ 1 \\ -\frac{\delta F_{BT}^*}{\alpha_3 + \delta A_{BT}^* - C_{BT2}} \end{pmatrix}, \quad T^{-1}BT = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \chi_3 \end{pmatrix}.$$

Then, $T^{-1} = (Z_1^T, Z_2^T, Z_0^T)^T$, here $Z_2^T B = 0$, $Z_1^T B = Z_2^T$, i.e., Z_1 , Z_2 are the left generalized eigenvectors of *B* corresponding to the eigenvalue $\chi = 0$ and Z_0 contains the left generalized eigenvectors of the matrix (χ_3).

We get

$$\begin{split} Z_1 &\triangleq \begin{pmatrix} Z_{11} \\ Z_{12} \\ Z_{13} \end{pmatrix} = \begin{pmatrix} -\frac{1}{L_2}(1 + \frac{L_4 - L_1 L_3 L_4}{L_1 - L_4}) \\ -\frac{L_1 L_4}{L_1 - L_4} \end{pmatrix}, \quad Z_2 \triangleq \begin{pmatrix} Z_{21} \\ Z_{22} \\ Z_{23} \end{pmatrix} = \begin{pmatrix} \frac{1}{L_2} \\ 0 \\ 0 \end{pmatrix}, \\ Z_0 &\triangleq \begin{pmatrix} Z_{01} \\ Z_{02} \\ Z_{03} \end{pmatrix} = \begin{pmatrix} \frac{1 - L_1 L_3 L_4}{L_1 - L_4} \\ \frac{L_1}{L_1 - L_4} \\ \frac{L_1}{L_4 - L_1} \end{pmatrix}, \end{split}$$

where

$$L_{1} = -\frac{\alpha_{3} + \delta A_{BT}^{*}}{\delta F_{BT}^{*}}, \ L_{2} = \frac{\beta}{\lambda_{2}m} - \frac{\alpha_{3} + \delta A_{BT}^{*}}{\delta \lambda_{2}m F_{BT}^{*} A_{BT}^{*}}, \ L_{3} = -\frac{\alpha_{3} + \delta A_{BT}^{*} + 1}{\delta F_{BT}^{*}},$$
$$L_{4} = -\frac{\delta F_{BT}^{*}}{\alpha_{3} + \delta A_{BT}^{*} - C_{BT2}}.$$

By using the notations in Carrillo et al. (2010), we have

$$\begin{split} a &= \frac{1}{2} T_1^T (Z_2 \cdot D^2 F(U_0, \rho_0)) T_1 = \frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (\beta Z_{22} + \delta Z_{23} - k_{2BT} \beta Z_{21}), \\ b &= T_1^T (Z_1 \cdot D^2 F(U_0, \rho_0)) T_1 + T_1^T (Z_2 \cdot D^2 F(U_0, \rho_0)) T_2 \\ &= \frac{2(\alpha_3 + \delta A_{BT}^*)}{\delta F_{BT}^*} (\beta Z_{12} + \delta Z_{13} - k_{2BT} \beta Z_{11}) - L_2 \frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (m Z_{21} - \lambda_2 m Z_{22}) \\ &- L_3 (\beta Z_{22} + \delta Z_{23} - k_{2BT} \beta Z_{21}) + \frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (\beta Z_{22} + \delta Z_{23} - k_{2BT} \beta Z_{21}), \end{split}$$

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$$B_{0} = T_{0}\chi_{3}^{-1}Z_{0} = -\frac{1}{C_{BT2}} \begin{pmatrix} 0 & 0 & 0 \\ Z_{01} & Z_{02} & Z_{03} \\ L_{4}Z_{01} & L_{4}Z_{02} & L_{4}Z_{03} \end{pmatrix}, S_{1} = F_{\hat{\rho}}^{T}(U_{0}, \rho_{0})Z_{2} \triangleq \begin{pmatrix} S_{11} \\ S_{12} \end{pmatrix}$$
$$= \begin{pmatrix} Z_{21}\beta F_{BT}^{*}A_{BT}^{*} \\ -Z_{21}P_{BT}^{*} \end{pmatrix},$$
$$S_{2} = \begin{bmatrix} \frac{2a}{b} (T_{1}^{T}(Z_{1} \cdot D^{2}F(U_{0}, \rho_{0}))T_{2} + T_{2}^{T}(Z_{2} \cdot D^{2}F(U_{0}, \rho_{0}))T_{2}) \\ -T_{1}^{T}(Z_{2} \cdot D^{2}F(U_{0}, \rho_{0}))T_{2} \end{bmatrix} F_{\hat{\rho}}^{T}(U_{0}, \rho_{0})Z_{1}$$
$$- \frac{2a}{b} \sum_{i=1}^{2} (Z_{i} \cdot (F_{\hat{\rho}U}(U_{0}, \rho_{0}) - (B_{0}F_{\hat{\rho}}(U_{0}, \rho_{0}))^{T} \times D^{2}F(U_{0}, \rho_{0})))T_{i}$$

$$+ (Z_2 \cdot (F_{\hat{\rho}U}(U_0, \rho_0) - (B_0 F_{\hat{\rho}}(U_0, \rho_0))^T \times D^2 F(U_0, \rho_0)))T_1$$

= $\frac{2a}{b} H \begin{pmatrix} Z_{11} \beta F_{BT}^* A_{BT}^* \\ -Z_{13} P_{BT}^* \end{pmatrix} - \frac{2a}{b} Q + M \triangleq \begin{pmatrix} S_{21} \\ S_{22} \end{pmatrix},$

where

$$\begin{split} H &= -\frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (-mZ_{11} + \lambda_2 m Z_{12}) L_2 + (k_{2BT}\beta Z_{11} - \beta Z_{12} - \delta Z_{13}) L_3 \\ &- \frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (k_{2BT}\beta Z_{11} \\ &- \beta Z_{12} - \delta Z_{13}) + 2 (-mZ_{21} + \lambda_2 m Z_{22}) L_2 L_3 + (k_{2BT}\beta Z_{21} - \beta Z_{22} - \delta Z_{23}) L_3 \\ &- \frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (-mZ_{21} \\ &+ \lambda_2 m Z_{22}) L_2 - \frac{\alpha_3 + \delta A_{BT}^*}{\delta F_{BT}^*} (k_{2BT}\beta Z_{21} - \beta Z_{22} - \delta Z_{23}), \end{split}$$

$$\begin{aligned} \mathcal{Q} &= \frac{1}{C_{BT2}} \begin{pmatrix} L_1 Q_{12} + Q_{13} + L_2 q_{11} + L_3 q_{12} + q_{13} \\ L_1 Q_{22} + Q_{23} + L_2 q_{21} + L_3 q_{22} + q_{23} \end{pmatrix}, \ \mathcal{M} &= \frac{1}{C_{BT2}} \begin{pmatrix} L_1 q_{12} + q_{13} \\ L_1 q_{22} + q_{23} \end{pmatrix}, \end{aligned}$$

$$\begin{aligned} \mathcal{Q}_{12} &= Z_{11} (C_{BT2} \beta F_{BT}^* + L_4 Z_{01} \beta^2 F_{BT}^* A_{BT}^*) \\ &- L_4 Z_{12} Z_{01} \beta^2 F_{BT}^* A_{BT}^* - L_4 Z_{13} Z_{01} \delta \beta F_{BT}^* A_{BT}^*, \end{aligned}$$

$$\begin{aligned} \mathcal{Q}_{22} &= -Z_{11} Z_{01} L_4 k_{2BT} \beta P_{BT}^* + Z_{12} Z_{01} L_4 \beta P_{BT}^* + Z_{13} Z_{01} L_4 \delta P_{BT}^*, \end{aligned}$$

$$\begin{aligned} \mathcal{Q}_{13} &= Z_{11} (C_{BT2} \beta A_{BT}^* + Z_{01} \beta^2 k_{2BT} F_{BT}^* A_{BT}^*) - Z_{12} Z_{01} \beta^2 F_{BT}^* A_{BT}^*, \end{aligned}$$

$$\begin{aligned} \mathcal{Q}_{23} &= -Z_{11} Z_{01} k_{2BT} \beta P_{BT}^* + Z_{12} Z_{01} \beta P_{BT}^* + Z_{13} Z_{01} \delta P_{BT}^*, \end{aligned}$$

$$\begin{aligned} \mathcal{Q}_{23} &= -Z_{11} Z_{01} k_{2BT} \beta P_{BT}^* + Z_{12} Z_{01} \beta P_{BT}^* + Z_{13} Z_{01} \delta P_{BT}^*, \end{aligned}$$

$$\begin{aligned} \mathcal{Q}_{11} &= -Z_{11} Z_{01} m \beta F_{BT}^* A_{BT}^* + Z_{12} Z_{01} m \lambda_2 \beta F_{BT}^* A_{BT}^*, \end{aligned}$$

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$$q_{12} = Z_{21}(C_{BT2}\beta F_{BT}^* + L_4 Z_{01}\beta^2 F_{BT}^* A_{BT}^*) - L_4 Z_{22} Z_{01}\beta^2 F_{BT}^* A_{BT}^* - L_4 Z_{23} Z_{01}\delta\beta F_{BT}^* A_{BT}^*,$$

$$q_{22} = -Z_{21} Z_{01} L_4 k_{2BT}\beta P_{BT}^* + Z_{22} Z_{01} L_4 \beta P_{BT}^* + Z_{23} Z_{01} L_4 \delta P_{BT}^*,$$

$$q_{13} = Z_{21}(C_{BT2}\beta A_{BT}^* + Z_{01}\beta^2 k_{2BT} F_{BT}^* A_{BT}^*) - Z_{22} Z_{01}\beta^2 F_{BT}^* A_{BT}^* - Z_{23} Z_{01}\delta\beta F_{BT}^* A_{BT}^*,$$

$$q_{23} = -Z_{21} Z_{01} k_{2BT}\beta P_{BT}^* + Z_{22} Z_{01}\beta P_{BT}^* + Z_{23} Z_{01}\delta P_{BT}^*.$$

Assume that

$$\begin{cases} \psi_1 = k_2 - k_{2BT}, \\ \psi_2 = \alpha_1 - \alpha_{1BT}. \end{cases}$$

Then

$$\begin{cases} \zeta_1 = S_1^T (\hat{\rho} - \rho_0) = S_{11} \psi_1 + S_{12} \psi_2, \\ \zeta_2 = S_2^T (\hat{\rho} - \rho_0) = S_{21} \psi_1 + S_{22} \psi_2. \end{cases}$$

According to Carrillo et al. (2010), for given nonlinear system (3.3), there exists (U_0, ρ_0) which satisfies the conditions:

(BT1) $F(U_0, \rho_0) = 0;$ (BT2) $\sigma[DF(U_0, \rho_0)] = \{\chi_{1,2} = 0; \operatorname{Re}(\chi_3) \neq 0\}$ (non-hyperbolicity); (BT3) $ab \neq 0$ (non-degeneracy); (BT4) S_1 and S_2 are linearly independent (transversality).

The topological behavior of the trajectories on the central manifold of system (3.3) near the Bogdanov-Takens bifurcation point (U_0, ρ_0) is locally topologically equivalent to the trajectory structure of the following system:

$$\begin{cases} \dot{x_1} = x_2, \\ \dot{x_2} = \zeta_1 + \zeta_2 x_1 + a x_1^2 + b x_1 x_2 = (S_{11}\psi_1 + S_{12}\psi_2) + (S_{21}\psi_1 + S_{22}\psi_2) x_1 \\ + a x_1^2 + b x_1 x_2. \end{cases}$$
(7.16)

Then we introduce a new time \overline{t} and new variables X_1 and X_2 given by

$$t = -\frac{b}{a}\bar{t}, \ x_1 = \frac{a}{b^2}X_1, \ x_2 = -\frac{a^2}{b^3}X_2.$$

System (7.16) can be rewritten as the following form

$$\begin{cases} \dot{X_1} = X_2, \\ \dot{X_2} = \bar{\zeta_1} + \bar{\zeta_2}X_1 + X_1^2 - X_1X_2, \end{cases}$$

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where

$$\bar{\zeta_1} = \frac{b^4}{a^3}(S_{11}\psi_1 + S_{12}\psi_2), \ \bar{\zeta_2} = \frac{b^2}{a^2}(S_{21}\psi_1 + S_{22}\psi_2).$$

If det $\left(\frac{\partial(\bar{\zeta}_1,\bar{\zeta}_2)}{\partial(k_2,\alpha_1)}\right)\Big|_{(k_2,\alpha_1)=(k_{2BT},\alpha_{1BT})} \neq 0$, then the parameter transformation is an invertible smooth change of parameters near the $(P_{BT}^*, A_{BT}^*, F_{BT}^*)$. Based on the discussions above and the results in Carrillo et al. (2010), we obtain the results stated in Theorem 3.8. The proof is complete.

The proof of Theorem 3.10 Let us consider a positive solution $(N(t), P(t), A(t), F(t))^T$ of system (2.1) with (2.2). For all t > 0, denote

$$M(t) = \lambda_1 N(t) + \lambda_2 P(t) + A(t) + \frac{(\lambda_1 k_1 + \lambda_2 k_2)\beta}{\delta} F(t),$$

and $\delta_m = \min\{\alpha_0, \alpha_1, \alpha_2, \alpha_3\}$. Then

$$\lim_{t \to \infty} \sup M(t) \le \frac{\lambda_1 (1 - \pi)q + \lambda_2 \pi q + \frac{(\lambda_1 k_1 + \lambda_2 k_2)\beta\omega}{\delta_m}}{\delta_m} := \gamma$$

From (2.1b) and (2.1d), we obtain

$$\lim_{t \to \infty} \inf P(t) \ge \frac{\pi q}{\alpha_1 + m\gamma} = \nu_2, \ \lim_{t \to \infty} \inf F(t) \ge \frac{\omega}{\alpha_3 + \delta \frac{\omega}{\alpha_3}} = \nu_4.$$

If $R_0 > 1$, there is only a $\theta > 0$ such that $\lambda_1 \mu \frac{(1-\pi)q}{\alpha_0+\mu\theta} + \lambda_2 m \frac{\pi q}{\alpha_1+m\theta} = \alpha_2 + \beta \frac{\omega}{\alpha_3}$. Thus, if $0 < \theta_2 < \theta_1 < \theta$, there exists a $\rho_0 > 0$ such that

$$\kappa = \lambda_1 \mu \frac{(1-\pi)q}{\alpha_0 + \mu \theta_1} + \lambda_2 m \frac{\pi q}{\alpha_1 + m \theta_1} - \alpha_2 - \left(\beta \frac{\omega}{\alpha_3} + \rho_0\right) > 0.$$

Next, let us show that

$$\lim_{t \to \infty} \inf A(t) \ge \theta_2 e^{-[\alpha_2 + \beta(\frac{\omega}{\alpha_3} + \rho_0)]d} = \upsilon_3.$$

Define

$$V = \lambda_1 \mu N A + \lambda_2 m P A - \alpha_2 A - \beta F A.$$

Claim: For any $t_0 > 0$, it is impossible to satisfy $A(t) \le \theta_2$ for all $t \ge t_0$.

By way of contradiction, there exists a $t_0 > 0$ such that $A(t) \le \theta_2$ for any $t \ge t_0$. From the first and second equations of system (2.1), one gets $\dot{N} \ge (1 - \pi)q - (\alpha_0 + \mu\theta_2)N$, $\dot{P} \ge \pi q - (\alpha_1 + m\theta_2)P$. Thus we get

$$\lim_{t \to \infty} \inf N(t) \ge \frac{(1-\pi)q}{\alpha_0 + \mu\theta_2} > \frac{(1-\pi)q}{\alpha_0 + \mu\theta_1}, \lim_{t \to \infty} \inf P(t) \ge \frac{\pi q}{\alpha_1 + m\theta_2} > \frac{\pi q}{\alpha_1 + m\theta_1}$$

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Hence, there exists a $T_1 > 0$ such that

$$N(t) \ge \frac{(1-\pi)q}{\alpha_0 + \mu\theta_1}, \text{ for all } t \ge t_0 + T_1.$$

Similarly, there is a $T_2 > 0$ satisfying

$$P(t) \ge \frac{\pi q}{\alpha_1 + m\theta_1}$$
, for all $t \ge t_0 + T_2$.

In addition, from the fourth equation of system (2.1), we get $\lim_{t\to\infty} \sup F(t) \leq \frac{\omega}{\alpha_3}$.

Then there exists a $T_3 > 0$ such that $F(t) \le \frac{\omega}{\alpha_3} + \rho_0$, for all $t \ge t_0 + T_3$. Set

$$\underline{A} = A(t_0 + d) > 0.$$

Now verify $A(t) \ge \underline{A} > 0$ for all $t \ge t_0 + \max\{T_1, T_2, T_3\} := \hat{\sigma}$. In fact, if there exists T > 0 such that for $\hat{\sigma} \le t \le \hat{\sigma} + T$, there is

$$A(t) \ge \underline{A}, \ A(\hat{\sigma} + T) = \underline{A}, \ A(\hat{\sigma} + T) \le 0,$$

it follows from the third equation of system (2.1) that

$$\dot{A}(\hat{\sigma}+T) = (\lambda_1 \mu N + \lambda_2 m P - \alpha_2 - \beta F) A(\hat{\sigma}+T)$$

$$\geq \left[\lambda_1 \mu \frac{(1-\pi)q}{\alpha_0 + \mu \theta_1} + \lambda_2 m \frac{\pi q}{\alpha_1 + m \theta_1} - \alpha_2 - \beta \left(\frac{\omega}{\alpha_3} + \rho_0\right) \right]$$

$$\underline{A} = \kappa \underline{A} > 0.$$

This is a contradiction to $\hat{A}(\hat{\sigma} + T) \leq 0$. Therefore, $A(t) \geq \underline{A}$ for all $t \geq \hat{\sigma} + T$. Hence, for all $t \geq \hat{\sigma} + T$, it follows from

$$\dot{V}(\hat{\sigma}+T) \ge \left[\lambda_1 \mu \frac{(1-\pi)q}{\alpha_0 + \mu\theta_1} + \lambda_2 m \frac{\pi q}{\alpha_1 + m\theta_1} - \alpha_2 - \beta \left(\frac{\omega}{\alpha_3} + \rho_0\right)\right] \underline{A} = \kappa \underline{A} > 0$$

that $V(t) \to \infty$ as $t \to \infty$, which also leads to a contradiction. The claim is proved. Next, we consider the following two cases:

- $A(t) \ge \theta_2$ holds for all sufficiently *t*;
- A(t) oscillates about θ_2 for all sufficiently t.

Clearly, we only need to consider the second case. Let t_1 , t_2 be large enough such that $t^* < t_1 < t_2$ and $A(t_1) = A(t_2) = \theta_2$, $A(t) < \theta_2(t_1 < t < t_2)$.

Consider that t_1, t_2 are sufficiently large, so $F(t) \le \frac{\omega}{\alpha_3} + \rho_0$ for all $t_1 < t < t_2$. From the first and second equations of system (2.1), we get $\dot{N}(t) \ge (1-\pi)q - \alpha_0 N -$ $\mu N\theta_2$, $\dot{P}(t) \ge \pi q - \alpha_1 P - m P\theta_2$, which implies that

$$\begin{split} N(t) &\geq \frac{(1-\pi)q}{\alpha_0 + \mu\theta_2} + \left[N(t_1) - \frac{(1-\pi)q}{\alpha_0 + \mu\theta_2} \right] e^{-(\alpha_0 + \mu\theta_2)(t-t_1)} \\ &\geq [1-e^{-(\alpha_0 + \mu\theta_2)(t-t_1)}] \frac{(1-\pi)q}{\alpha_0 + \mu\theta_2}, \\ P(t) &\geq \frac{\pi q}{\alpha_1 + m\theta_2} + \left[P(t_1) - \frac{\pi q}{\alpha_1 + m\theta_2} \right] e^{-(\alpha_1 + m\theta_2)(t-t_1)} \\ &\geq [1-e^{-(\alpha_1 + m\theta_2)(t-t_1)}] \frac{\pi q}{\alpha_1 + m\theta_2}, \text{ for all } t_1 < t < t_2 \end{split}$$

If $t_2 - t_1 \le d := \max\{T_1, T_2\}$, it follows from system (2.1) that

$$\dot{A}(t) \ge -\alpha_2 A - \beta \left(\frac{\omega}{\alpha_3} + \rho_0\right) A,$$

which implies that

$$A(t) \ge A(t_1)e^{-[\alpha_2 + \beta(\frac{\omega}{\alpha_3} + \rho_0)](t-t_1)} \ge \theta_2 e^{-[\alpha_2 + \beta(\frac{\omega}{\alpha_3} + \rho_0)]d}$$

It is obvious that

$$\lim_{t \to \infty} \inf A(t) \ge \theta_2 e^{-[\alpha_2 + \beta(\frac{\omega}{\alpha_3} + \rho_0)]d} = \upsilon_3, \text{ for } t \in (t_1, t_2).$$

If $t_2 - t_1 > d$, it is easily to get $A(t) \ge v_3$ for $t \in [t_1, t_1 + d]$. Then, as the proof of the above claim, we can show that $A(t) \ge v_3$ for $t_1 + d \le t \le t_2$. In fact, if not, there exists a $T^* \ge 0$, such that $A(t) \ge v_3$ for $t_1 + d \le t \le t_1 + d + T^*$, $A(t_1 + d + T^*) = v_3$ and $\dot{A}(t_1 + d + T^*) \le 0$. From the first and second equations of system (2.1), for $t_1 + d \le t \le t_1 + d + T^* \le t_2$, it follows $\dot{N}(t) \ge (1 - \pi)q - (\alpha_0 + \mu\theta_2)N(t)$, $\dot{P}(t) \ge \pi q - (\alpha_1 + m\theta_2)P(t)$, which implies

$$\begin{split} N(t) &\geq [1 - e^{-(\alpha_0 + \mu\theta_2)d}] \frac{(1 - \pi)q}{\alpha_0 + \mu\theta_2} \\ &\geq [1 - e^{-(\alpha_0 + \mu\theta_2)T_1}] \frac{(1 - \pi)q}{\alpha_0 + \mu\theta_2} \\ &= \frac{(1 - \pi)q}{\alpha_0 + \mu\theta_1}, \\ P(t) &\geq [1 - e^{-(\alpha_1 + m\theta_2)d}] \frac{\pi q}{\alpha_1 + m\theta_2} \\ &\geq [1 - e^{-(\alpha_1 + m\theta_2)T_2}] \frac{\pi q}{\alpha_1 + m\theta_2} \\ &= \frac{\pi q}{\alpha_1 + m\theta_1}, \end{split}$$

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for $t_1 + d \le t \le t_1 + d + T^* \le t_2$. From the third equation of system (2.1), it follows

$$\dot{A}(t_1+d+T^*) \ge \left[\lambda_1 \mu \frac{(1-\pi)q}{\alpha_0+\mu\theta_1} + \lambda_2 m \frac{\pi q}{\alpha_1+m\theta_1} - \alpha_2 - \beta(\frac{\omega}{\alpha_3}+\rho_0)\right] A(t_1+d+T^*) = \kappa \upsilon_3 > 0.$$

This is a contradiction to $\dot{A}(t_1 + d + T^*) \le 0$. Therefore, we have that $A(t) \ge \upsilon_3$ for $t \in [t_1, t_2]$. Consider the interval $[t_1, t_2]$ is chosen in an arbitrary way, then we can conclude that $A(t) \ge \upsilon_3$ for all large *t* for the second case. Hence, $\lim_{t\to\infty} \inf A(t) \ge \upsilon_3$. The proof is complete.

The proof of Theorem 5.1 Let $r \in (0, 1)$, $x(t) = (\dot{N}, \dot{P}, \dot{A}, \dot{F})$ and $u, v \in \mathcal{U}$, one denotes the integrand

$$J(t, x(t), u) = A_1 N + A_2 P + A_3 A + \frac{1}{2} B_1 u_1^2 + \frac{1}{2} B_2 u_2^2,$$

and obtains

$$J(t, x(t), (1-r)u + rv) - (1-r)J(t, x(t), u) - rJ(t, x(t), v)$$

= $r(r-1)\left[\frac{1}{2}B_1(u_1 - v_1)^2 + \frac{1}{2}B_2(u_2 - v_2)^2\right] \le 0$

so the integrand J is convex on the control set \mathscr{U} . We easily seek out some positive numbers ω_1, ω_2 and ξ such that the integrand of the objective function J(u) means

$$J(u) \ge \omega_1 |u|^{\xi} - \omega_2 \left(\omega_1 = \frac{B_i}{2}, \xi = 2 \right).$$

The proof is complete.

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