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GLOBAL DYNAMICS OF TWO PHYTOPLANKTON-ZOOPLANKTON MODELS WITH TOXIC SUBSTANCES EFFECT*

Shanshan Chen[1], Hong Yang[1] and Junjie Wei[1,2,†]

Abstract In this paper, we investigate phytoplankton-zooplankton models with toxic substances effect and two different kinds of predator functional responses. For Holling type II predator functional response, it is shown that the local stability of the positive equilibrium implies global stability if there exists a unique positive equilibrium. When there exist multiple positive equilibria, the local stability of the positive equilibrium with small phytoplankton population density implies that the model occurs bistable phenomenon. These results also hold for Holling type III predator functional response under certain conditions.

Keywords Phytoplankton-zooplankton, global stability, bistable phenome -non.

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1. Introduction

During the past half century, the interaction between the phytoplankton and zooplankton has been investigated extensively, and it is also well established that a great number of phytoplankton species produce toxin, which affects the growth of the zooplankton species, see [7]. Then various models described by ODEs, PDEs, and DDEs have been built and investigated to understand this interaction, see [2, 3, 11, 12, 15, 16, 19, 21, 23, 24, 29–31] and references therein. For example, Chattopadhyay et al. [3] proposed the following ODE model

$$\begin{cases} \dfrac{\mathrm{d}P}{\mathrm{d}t} = bP\left(1-\dfrac{P}{k}\right) - \alpha f(P)Z, \\ \dfrac{\mathrm{d}Z}{\mathrm{d}t} = \beta f(P)Z - rZ - \theta g(P)Z, \end{cases} \tag{1.1}$$

to show the effect of toxic substances. They analyzed the local stability of model (1.1) with different kinds of $f(u)$ and $g(u)$, and showed theoretically and

†the corresponding author. Email address:weijj@hit.edu.cn(J. Wei)
[1]Department of Mathematics, Harbin Institute of Technology, Weihai, Shandong, 264209, China
[2]School of Mathematics and Big Data, Foshan University, Foshan, Guangdong, 528000, China
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numerically that the release of toxic substances by TPP (toxin-producing plankton) can terminate the planktonic blooms. Here P represents the density of the TPP population; Z is the density of the zooplankton population; $\alpha > 0$ and $\beta > 0$ represent the predation and conversion rates of the zooplankton on the TPP population, respectively; $b > 0$ and $k > 0$ are the intrinsic growth rate and carry capacity of the TPP, respectively; $r > 0$ is the death rate of the zooplankton population; $f(P)$ represents the predator functional response. We should point out that $g(P)$ represents the distribution of the toxin substances, and $\theta > 0$ denotes the rate of toxin liberation by the TPP population.

There are also some other models considering toxin effect, such as a plant-herbivore model with toxin-determined functional response [6]. Liu et al. [14] studied the Hopf and homoclinic bifurcations of the model, and then Castillo-Chavez et al. [1] showed that the local stability of one positive equilibrium implies global stability or bistable phenomenon under different conditions. Recently, Zhao et al. [32] generalized the results in [14] and deduced that a limit cycle is generated in a supercritical Hopf bifurcation and terminated in a homoclinic bifurcation, as the parameters vary. Zhang and Yan [28] showed the occurrence of Hopf bifurcation of spatially inhomogeneous periodic solutions for the corresponding diffusive model.

In this paper, we revisit model (1.1). Choosing $f(u) = \dfrac{u^h}{1+cu^h}$ (for $h = 1, 2$) and $g(u) = u$ for simplicity, we have the following system: (see also Cases 5 and 7 in [3])

$$\begin{cases} \dfrac{\mathrm{d}P}{\mathrm{d}t} = bP\left(1 - \dfrac{P}{k}\right) - \dfrac{\alpha P^h Z}{1+cP^h}, & t > 0, \\ \dfrac{\mathrm{d}Z}{\mathrm{d}t} = \dfrac{\beta P^h Z}{1+cP^h} - rZ - \theta PZ, & t > 0, \\ P(0) = P_0 \geq 0, \quad Z(0) = Z_0 \geq 0. \end{cases} \tag{1.2}$$

Here, for $h = 1$, $f(u)$ denotes the Holling type II predator functional response, and for $h = 2$, $f(u)$ denotes the Holling type III predator functional response. By using the following rescaling,

$$\tilde{t} = bt, \quad \tilde{u} = \frac{P}{k}, \quad \tilde{v} = \frac{\alpha k^{h-1} Z}{b}, \quad \tilde{c} = ck^h, \quad \tilde{\beta} = \frac{\beta k^h}{b}, \quad \tilde{r} = \frac{r}{b}, \quad \tilde{\theta} = \frac{\theta k}{b},$$

and dropping the tilde sign, system (1.2) can be simplified as follows:

$$\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = u\,(1-u) - \dfrac{u^h v}{(1+cu^h)}, & t > 0, \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = \dfrac{\beta u^h v}{(1+cu^h)} - rv - \theta uv, & t > 0, \\ u(0) = u_0 \geq 0, \quad v(0) = v_0 \geq 0. \end{cases} \tag{1.3}$$

Here parameters β, r, θ and c are positive, $h = 1, 2$, and θ denotes the effect of the toxin substances, (more detailed biological meaning can be found in [3, 23]). If $\theta = 0$ and $h = 1$, then system (1.3) is reduced to the classical Rosenzweig-MacArthur model, and has been extensively studied in the existing literature, see for example [5, 8, 9]. The dynamics and bifurcations for the corresponding diffusive model could be found in [13, 18, 27, 33]. For $\theta = 0$ and $h = 2$, the global dynamics of system (1.3)

were investigated in [4, 10, 22]. See also [17, 20, 25, 26, 34] for predator-prey models with nonmonotonic predator functional response.

In this paper, we mainly investigate the effect of the toxin substances and show the occurrence of global stable and bistable phenomenons for model (1.3). The rest of the paper is organized as follows. In Section 2, we investigate the global dynamics of system (1.3). In Section 3, some numerical simulations are illustrated to support the obtained results. We also remark that, by virtue of the obtained results, the local Hopf bifurcation results in [23] can be improved and the global Hopf bifurcation results can be obtained.

2. Global dynamics

Firstly, we show that system (1.3) is dissipative.

Lemma 2.1. *For any initial value* (u_0, v_0)*, where* $u_0, v_0 > 0$*, the corresponding solution of system* (1.3) *is positive and bounded.*

Proof. It follows from the comparison principle that $u(t), v(t) > 0$. Then $u'(t) \leq u\,(1-u)$, which yields $u(t) \leq \max\{u_0, 1\}$ for all $t \geq 0$. Therefore, $[\beta u(t) + v(t)]' \leq \beta(1+r)\max\{u_0, 1\} - r(\beta u(t) + v(t))$, which implies that

$$\beta u(t) + v(t) \leq \max\left\{\beta u_0 + v_0, \frac{\beta(1+r)}{r}\max\{u_0, 1\}\right\}$$

for all $t \geq 0$. This completes the proof. □

Clearly, system (1.3) always has two nonnegative equilibria $(0, 0)$ and $(1, 0)$. An easy calculation implies that (u, v) is a positive equilibrium of system (1.3) if and only if $u \in (0, 1)$ is a solution of the following equation

$$\beta = \Psi(u) := \frac{(r+\theta u)(1+cu^h)}{u^h} \quad \text{for} \quad h = 1, 2. \tag{2.1}$$

Clearly, it can be to see

1. there exists $\overline{u} > 0$ such that $\Psi'(\overline{u}) = 0$, $\Psi'(u) > 0$ for $u \in (\overline{u}, \infty)$, and $\Psi'(u) < 0$ for $u \in (0, \overline{u})$;
2. $\lim_{u\to 0}\Psi(u) = \infty$, $\lim_{u\to 1}\Psi(u) = (c+1)(r+\theta)$.

For $h = 1$, one can easily check that $\overline{u} = \sqrt{\frac{r}{c\theta}}$, and for $h = 2$, $\overline{u}$ is the unique positive root of the following equation

$$\theta c x^3 - \theta x - 2r = 0. \tag{2.2}$$

Then we have the following two results on the number of positive equilibria.

Lemma 2.2. *Assume that* $\overline{u} \geq 1$*. Then system* (1.3) *has no positive equilibrium for* $\beta \in (0, (c+1)(r+\theta))$*, and a unique positive equilibrium for* $\beta \in ((c+1)(r+\theta), \infty)$*.*

Lemma 2.3. *Assume that* $\overline{u} < 1$*. Then system* (1.3) *has no positive equilibrium for* $\beta \in (0, \Psi(\overline{u}))$*, a unique positive equilibrium* (u_-, v_-) *for* $\beta \in ((c+1)(r+\theta), \infty)$*, and two positive equilibria for* $\beta \in (\Psi(\overline{u}), (c+1)(r+\theta))$*.*

For the case of $h = 1$, one can easily check that $\Psi(u) = \beta$ has two roots denoted by

$$u_{\pm} = \frac{-(\theta + cr - \beta) \pm \sqrt{(\theta + cr - \beta)^2 - 4c\theta r}}{2\theta c}. \tag{2.3}$$

Define

$$v_{\pm} = (1 - u_{\pm})(1 + cu_{\pm}), \tag{2.4}$$

and (u_+, v_+) (respectively, (u_-, v_-)) is a positive equilibrium of system (1.3) if and only if $u_+ \in (0, 1)$ (respectively, $u_- \in (0, 1)$). For simplicity of the notations, if system (1.3) has a unique positive equilibrium, we denote it by (u_-, v_-), and if there exist two positive equilibria, we denote them by (u_-, v_-) and (u_+, v_+), where $u_- < u_+$.

Now, we consider the stability of the nonnegative equilibria of system (1.3). Clearly, the stability of nonnegative equilibria $(0, 0)$ and $(1, 0)$ can be summarized as follows.

1. At $(0, 0)$, the eigenvalues of the Jacobian matrix are $\mu_1 = 1$ and $\mu_2 = -r$. Therefore, $(0, 0)$ ia always a saddle, the v-axis is the stable manifold of $(0, 0)$, and the unstable manifold of $(0, 0)$ is along the u-axis.
2. At $(1, 0)$, the eigenvalues of the Jacobian matrix are $\mu_1 = -1$ and $\mu_2 = \frac{\beta}{1+c} - r - \theta$. Therefore, if $\beta > (1 + c)(r + \theta)$, then $(1, 0)$ is a saddle, and the stable manifold of $(1, 0)$ is the positive part of u-axis. If $\beta < (1 + c)(r + \theta)$, then $(1, 0)$ is a stable node.

Then, Lemmas 2.1-2.3 and the Poincaré-Bendixson theorem imply that $(1, 0)$ is globally attractive when system (1.3) has no positive equilibrium.

Theorem 2.1. *Assume that one of the following assumptions is satisfied:*

(1) $\overline{u} \geq 1$ *and* $\beta \in (0, (c + 1)(r + \theta))$,

(2) $\overline{u} < 1$ *and* $\beta \in (0, \Psi(\overline{u}))$.

Then system (1.3) *has no positive equilibrium, and for any positive initial value* (u_0, v_0)*, the corresponding solution of system* (1.3) *converges to the equilibrium* $(1, 0)$ *as* $t \to \infty$,

We remark that for $h = 1$, $\overline{u} = \sqrt{\frac{r}{c\theta}}$ and $B(\overline{u}) = \theta\left(1 + \sqrt{\frac{cr}{\theta}}\right)^2$, and for $h = 2$, $\overline{u}$ is the unique positive root of Eq. (2.2). In the following, we consider the dynamics of system (1.3) when it has positive equilibrium. As illustrated in Lemmas 2.2 and 2.3, there are two possible cases:

($\tilde{I}_1$) system (1.3) has only one positive equilibrium (u_-, v_-). That is, $\beta > (c + 1)(r + \theta)$.

($\tilde{I}_2$) system (1.3) has two positive equilibria $(u_{\pm}, v_{\pm})$, where $u_- < u_+$. That is, $\overline{u} < 1$ and $\beta \in (\Psi(\overline{u}), (c + 1)(r + \theta))$.

For the simplicity of notations, we denote

$$\phi(u) = \frac{u^h}{1 + cu^h}, \quad g(u) = \frac{(1 - u)(1 + cu^h)}{u^{h-1}} \quad \text{for} \quad h = 1, 2. \tag{2.5}$$

A direct computation implies that the Jocobian matrix of system (1.3) at equilibrium $(u_\pm, v_\pm)$ is as follows:

$$J((u_\pm, v_\pm)) = \begin{bmatrix} \phi(u_\pm)g'(u_\pm) & -\phi(u_\pm) \\ (\beta\phi'(u_\pm) - \theta)v_\pm & 0 \end{bmatrix}.$$

Therefore, positive equilibrium (u_+, v_+) is a saddle point if it exists, and positive equilibrium (u_-, v_-) is not a saddle point. Moreover, (u_-, v_-) is stable if $g'(u_-) < 0$, and unstable if $g'(u_-) > 0$.

Here we only consider the case that (u_-, v_-) is stable, that is, $g'(u_-) < 0$. We will analyze whether the local stability of equilibrium (u_-, v_-) implies the global stable or bistable phenomenon. As in [1], we denote

$$M(u) = \beta - \Psi(u), \tag{2.6}$$

where $\Psi(u)$ is defined as in Eq. (2.1). Then system (1.3) with positive initial value (u_0, v_0) can be rewritten as

$$\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = \phi(u)[g(u) - v], & t > 0, \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = \phi(u)M(u)v, & t > 0, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \tag{2.7}$$

and $(\tilde{I}_1)$ and $(\tilde{I}_2)$ are equivalent to the following (I_1) and (I_2), respectively,

(I_1) $M(u_-) = 0$, $M(u) < 0$ for $u \in (0, u_-)$, and $M(u) > 0$ for $u \in (u_-, 1]$;

(I_2) $M(u_-) = M(u_+) = 0$, $M(u) < 0$ for $u \in (0, u_-) \cup (u_+, 1)$, and $M(u) > 0$ for $u \in (u_-, u_+)$.

We see that system (2.7) takes the same form as system (3.1) in [1], but $\phi(u)$, $g(u)$ and $M(u)$ are different. Especially, $g(u)$ changes its monotonicity at most once for system (3.1) in [1], but here for $h = 2$, $g'(u)$ can have two zeros, and the monotonicity of $g(u)$ is divided into two cases:

(a_1) $g(u)$ is strictly decreasing;

(a_2) There exist

$$u_1, u_2 \in (0, 1) \text{ such that } g'(u_1) = g'(u_2) = 0, \tag{2.8}$$

and $g'(u) < 0$ for $u \in (0, u_1) \cup (u_2, 1)$, $g'(u) > 0$ for $u \in (u_1, u_2)$.

We denote

$$\overline{u}_1 = \{\lambda \in (0, u_1) : g(\lambda) = g(u_2)\} \tag{2.9}$$

if $g(u)$ satisfies (a_2).

In the following, we will show that the method in [1] can also be applied to system (1.3) to prove the nonexistence of periodic orbit and homoclinic orbit. Define a function

$$\xi = G(u) = \int_{u_-}^{u} |M(s)|\mathrm{d}s \text{ for } u \in (0, u^*], \tag{2.10}$$

where $u^* = 1$ for case (I_1) and $u^* = u_+$ for case (I_2). Noticing that $\lim_{u\to 0^+} |M(u)|u^h = r$, we have $\lim_{u\to 0^+} G(u) = -\infty$. It follows that $G(u)$ is strictly increasing and has a inverse function

$$\theta(\xi) = G^{-1}(\xi) \text{ with domain } (-\infty, \xi^*], \tag{2.11}$$

where

$$\xi^* = G(u^*). \tag{2.12}$$

The following result is from [1], (see Proposition 3.2 in [1]), but we include here for the sake of completeness:

Theorem 2.2. *Assume that $M(u)$ satisfies (I_1) or (I_2), $\lim_{u\to 0^+} G(u) = -\infty$, and $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$, where $G(u)$, $\theta(\xi)$ and ξ^* are defined as in Eqs.* (2.10), (2.11) *and* (2.12) *respectively. Then system* (2.7) *has no closed orbit and homoclinic orbit in the region $\mathbf{R}^2_+ = \{(u, v) : u \geq 0, v \geq 0\}$.*

Therefore, the properties of function $g(\theta(\xi))$ are crucial for the global dynamics of system (1.3). Note that the monotonicity of $g(u)$ for $h = 1$ and $h = 2$ is different. We first consider the case that $h = 1$.

Theorem 2.3. *Assume that $\beta, r, \theta, c > 0$ and $h = 1$, one of assumptions (I_1) and (I_2) is satisfied, and $g'(u_-) < 0$. Then $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$, where ξ^* is defined as in Eq.* (2.12).

Proof. Obviously, for $\xi \in (0, \xi^*)$, $0 < \theta(-\xi) < u_- < \theta(\xi) < u^*$. If $g'(0) \leq 0$, then $g(u)$ is strictly decreasing, and consequently, $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$.

Now, we consider the case that $g'(0) > 0$. Then $c > 1$, and there exists $u_c := \frac{c-1}{2c}$ such that

$$g'(u) > 0 \text{ for } u \in (0, u_c), \quad g'(u) < 0 \text{ for } u \in (u_c, \infty), \text{ and } g'(u_c) = 0. \tag{2.13}$$

Since $g'(u_-) < 0$, it follows that $u_c \in (0, u_-)$. Let $\beta_0 = \Psi(u_c)$, denote

$$H_0(u) = \beta_0 - \Psi(u),$$

where Ψ is defined as in Eq. (2.1), and define an auxiliary function $\xi = G_0(u) = \int_{u_c}^{u} |H_0(u)| ds$ for $u \in (0, u^*]$. Clearly, G_0 also has an inverse function defined by $\theta_0(\xi) = G_0^{-1}(\xi)$ with domain $(-\infty, G_0(u^*)]$. Then the proof for the case of $g'(0) > 0$ is divided into three steps.

Step 1. We first show that $\dfrac{|g'(u_c + x)|}{|H_0(u_c + x)|}$ is strictly decreasing for $x \in (-u_c, u^*)$ and $x \neq 0$. Since $\Psi(u)$ is strictly decreasing for $u \in (0, u_-)$, we have

$$\beta_0 = \Psi(u_c) > \beta = \Psi(u_-), \tag{2.14}$$

which implies that $H_0(u_c + x) < 0$ for $x \in (-u_c, 0)$ and $H_0(u_c + x) > 0$ for $x \in (0, u^* - u_c)$. Clearly,

$$H_0(u_c + x) = x h_0(x),$$

where $h_0(x) := \left[\dfrac{r}{u_c(u_c + x)} - c\theta\right]$. It follows that

$$h_0(x) > 0 \text{ for } x \in (-u_c, u^* - u_c),$$

and $h_0(x)$ is strictly decreasing. Then, for $x \in (-u_c, u^* - u_c)$ and $x \neq 0$,

$$\frac{|g'(u_c + x)|}{|H_0(u_c + x)|} = \frac{2c}{h_0(x)},$$

which is strictly increasing.

Step 2. We show that, for any $\xi \in (0, G_0(u^*))$, $g(\theta_0(-\xi)) > g(\theta_0(\xi))$. Noticing that $\theta_0(G_0(u)) = u$, we have $\theta_0'(\xi) = \dfrac{1}{|H_0(\theta_0(\xi))|}$ for $\xi \in (0, G_0(u^*))$, and consequently,

$$\begin{aligned} g(\theta_0(\xi)) =& g(\theta_0(0)) + \int_0^{\xi} \frac{g'(\theta_0(s))}{|H_0(\theta_0(s))|} \mathrm{d}s, \\ g(\theta_0(-\xi)) =& g(\theta_0(0)) + \int_0^{-\xi} \frac{g'(\theta_0(s))}{|H_0(\theta_0(s))|} \mathrm{d}s. \end{aligned} \tag{2.15}$$

It follows from Eq. (2.13) that $g'(\theta_0(s)) < 0$, and $g'(\theta_0(-s)) > 0$ for $s > 0$. Then, by virtue of Eq. (2.15), we have

$$\begin{aligned} g(\theta_0(-\xi)) - g(\theta_0(\xi)) &= \int_0^{-\xi} \frac{g'(\theta_0(s))}{|H_0(\theta_0(s))|} \mathrm{d}s - \int_0^{\xi} \frac{g'(\theta_0(s))}{|H_0(\theta_0(s))|} \mathrm{d}s \\ &= -\int_0^{\xi} \frac{g'(\theta_0(-s))}{|H_0(\theta_0(-s))|} \mathrm{d}s - \int_0^{\xi} \frac{g'(\theta_0(s))}{|H_0(\theta_0(s))|} \mathrm{d}s \\ &= -\int_0^{\xi} \frac{|g'(\theta_0(-s))|}{|H_0(\theta_0(-s))|} \mathrm{d}s + \int_0^{\xi} \frac{|g'(\theta_0(s))|}{|H_0(\theta_0(s))|} \mathrm{d}s \\ &= -\int_0^{\xi} \frac{|g'(u_c + (\theta_0(-s) - u_c))|}{|H_0(u_c + (\theta_0(-s) - u_c))|} \mathrm{d}s + \int_0^{\xi} \frac{|g'(u_c + (\theta_0(s) - u_c))|}{|H_0(u_c + (\theta_0(s) - u_c))|} \mathrm{d}s. \end{aligned} \tag{2.16}$$

It follows from the results in Step 1 that $g(\theta_0(-\xi)) > g(\theta_0(\xi))$ for any $\xi \in (0, G_0(u^*))$.

Step 3. Finally, we show that $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$. Noticing that $\theta(-\xi) < u_- < \theta(\xi)$, $g(u)$ is strictly decreasing for $u \geq u_c$ and $u_- > u_c$, we have $g(\theta(-\xi)) > g(\theta(\xi))$ if $\theta(-\xi) \geq u_c$. Then we consider the case that $\theta(-\xi) < u_c$, and consequently, there exists $\xi_1 > 0$ such that

$$-\xi_1 = \int_{u_c}^{\theta(-\xi)} |H_0(s)| \mathrm{d}s = \int_{u_c}^{\theta(-\xi)} |\beta_0 - \Psi(s)| \mathrm{d}s, \tag{2.17}$$

which yields

$$\theta_0(-\xi_1) = \theta(-\xi). \tag{2.18}$$

Since $\beta_0 > \beta$ from Eq. (2.14) and $\beta_0 < \Psi(s)$ for $s \in (0, u_c)$, we have

$$\begin{aligned} -\xi_1 &= \int_{\theta(-\xi)}^{u_c} [\beta_0 - \Psi(s)] \mathrm{d}s \geq \int_{\theta(-\xi)}^{u_c} [\beta - \Psi(s)] \mathrm{d}s \\ &= \int_{\theta(-\xi)}^{u_-} [\beta - \Psi(s)] \mathrm{d}s + \int_{u_-}^{u_c} [\beta - \Psi(s)] \mathrm{d}s. \end{aligned} \tag{2.19}$$

Noticing that $\Psi(u) > \beta$ for $u \in (0, u_-)$ and $u_c < u_-$, we have $\int_{u_-}^{u_c} [\beta - \Psi(s)] ds > 0$. This, combined with Eq. (2.19), yields

$$-\xi_1 > -\int_{u_-}^{\theta(-\xi)} [\beta - \Psi(s)] \mathrm{d}s = \int_{u_-}^{\theta(-\xi)} |\beta - \Psi(s)| \mathrm{d}s = -\xi,$$

and consequently $\xi_1 < \xi < \xi^*$. Noting that

$$G_0(u^*) = \int_{u_c}^{u^*} |\beta_0 - \Psi(s)|\mathrm{d}s \geq \int_{u_-}^{u^*} |\beta - \Psi(s)|\mathrm{d}s = G(u^*) = \xi^*,$$

we deduce that ξ_1 is in the domain of $\theta_0(\xi)$. Therefore,

$$\int_{u_c}^{\theta_0(\xi_1)} |\beta_0 - \Psi(s)|\mathrm{d}s = \xi_1 < \xi = \int_{u_-}^{\theta(\xi)} |\beta - \Psi(s)|\mathrm{d}s \leq \int_{u_c}^{\theta(\xi)} |\beta - \Psi(s)|\mathrm{d}s,$$

which implies that $u_c < \theta_0(\xi_1) \leq \theta(\xi)$. It follows that

$$g(\theta(-\xi)) = g(\theta_0(-\xi_1)) > g(\theta_0(\xi_1)) \geq g(\theta(\xi)).$$

This completes the proof. □

Then, by virtue of Theorems 2.2, 2.3 and the Poincaré-Bendixson theorem, we have the following results on the global dynamics of model (1.3) for $h = 1$.

Theorem 2.4. *Assume that $\beta, r, \theta, c > 0$ and $h = 1$. Then*

1. *if (u_-, v_-) is the unique positive equilibrium of system (1.3) and $g'(u_-) < 0$, then for any positive initial value (u_0, v_0), the corresponding solution of system (1.3) converges to (u_-, v_-).*
2. *if system (1.3) has two positive equilibria (u_-, v_-) and (u_+, v_+), $(u_- < u_+)$ and $g'(u_-) < 0$, then (u_+, v_+) is a saddle point, and the stable manifold of (u_+, v_+) divides the first quadrant of $u - v$ plane into two subregions Ω_1 and Ω_2. The solutions with initial value in Ω_1 converge to (u_-, v_-), and that with initial value in Ω_2 converge to $(1, 0)$ as $t \to \infty$.*

From Theorem 2.4, we see that for $h = 1$, the local stability of (u_-, v_-) implies global stability if there exists a unique positive equilibrium (u_-, v_-). If there exist multiple positive equilibria, the local stability of (u_-, v_-) implies that the model occurs bistable phenomenon. For Holling type II predator functional response, toxin effect can induce bistable phenomenon.

Now we consider the case of $h = 2$. Since the monotonicity of $g(u)$ is different, the above mentioned results hold for Holling type III predator functional response under certain conditions.

Theorem 2.5. *Assume that $\beta, r, \theta, c > 0$, $h = 2$, one of assumptions (I_1) and (I_2) holds, and $g(u)$ satisfies (a_1) or satisfies (a_2) but $u_- \in (0, \overline{u}_1) \cup (u_2, 1)$, where u_2 and $\overline{u}_1$ are defined as in Eqs. (2.8) and (2.9) respectively. Then $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$, where ξ^* is defined as in Eq. (2.12).*

Proof. Obviously, for $\xi \in (0, \xi^*)$, $0 < \theta(-\xi) < u_- < \theta(\xi) < u^*$. If $g(u)$ satisfies (a_1), then $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$.

Now, we consider the case that $g(u)$ satisfies (a_2). That is, there exist $u_1, u_2 \in (0, 1)$ such that $g'(u_1) = g'(u_2) = 0$, $g'(u) < 0$ for $u \in (0, u_1) \cup (u_2, \infty)$, and $g'(u) > 0$ for $u \in (u_1, u_2)$. Clearly, if $u_- \in (0, \overline{u}_1)$, then $g(\theta(-\xi)) > g(\theta(\xi))$. Then we consider the case that $u_- \in \cup(u_2, 1)$. Let $\beta_2 = \Psi(u_2)$, denote

$$H_2(u) = \beta_2 - \Psi(u),$$

where Ψ is defined as in Eq. (2.1), and define a auxiliary function $\xi = G_2(u) = \int_{u_2}^{u} |H_2(u)|\mathrm{d}s$ for $u \in (0, u^*]$. Clearly, G_2 also has a inverse function defined by $\theta_2(\xi) = G_2^{-1}(\xi)$ with domain $(-\infty, G_2(u^*)]$.

Step 1. We first show that $\dfrac{|g'(u_2+x)|}{|H_2(u_2+x)|}$ is strictly decreasing for $x \in (u_1 - u_2, u^*)$ and $x \neq 0$. This is different from the case of $h = 1$, and we have no needs to show the monotonicity of the function for $u \in (-u_2, u_1 - u_2)$. Since $u_- > u_2$ and $\Psi(u)$ is strictly decreasing for $u \in (0, u_-)$, we have

$$\beta_2 = \Psi(u_2) > \beta = \Psi(u_-), \tag{2.20}$$

which implies that $H_2(u_2 + x) < 0$ for $x \in (-u_2, 0)$, and $H_2(u_2 + x) > 0$ for $x \in (0, u^* - u_2)$. Clearly, for $x \in (0, u^* - u_2)$ and $x \neq 0$,

$$H_2(u_2 + x) = x h_2(x),$$

where $h_2(x) := \dfrac{\Psi(u_2) - \Psi(u_2 + x)}{x}$, and

$$h_2(x) > 0 \ \text{ for } \ x \in (-u_2, u^* - u_2) \ \text{ and } \ x \neq 0.$$

A direct computation yields

$$\Psi''(u) = \frac{6r}{u^4} + \frac{2\theta}{u^3} > 0 \ \text{ for } \ u > 0. \tag{2.21}$$

Then it follows from the Taylor formula that there exists $\hat{x} > 0$ such that

$$h_2'(x) = \frac{-\Psi'(u_2 + x)x - \Psi(u_2) + \Psi(u_2 + x)}{x^2} = -\frac{\Psi''(\hat{x})}{2} < 0, \tag{2.22}$$

which implies that $h_2(x)$ is strictly decreasing. Denote

$$g_2(x) = -\frac{g'(u_2 + x)}{x} \ \text{ for } \ x \in (0, u^* - u_2) \ \text{ and } \ x \neq 0.$$

Since $g'(u_2 + x) < 0$ for $x > 0$, and $g'(u_2 + x) > 0$ for $x \in (u_1 - u_2, 0)$, we obtain that $g_2(x) > 0$ for $x \in (u_1 - u_2, u^* - u_2)$ and $x \neq 0$. Similarly, an easy computation implies that

$$g'''(u) = -\frac{6}{u^4} < 0.$$

and, by virtue of the Taylor formula, we see that there exists $\tilde{x} > 0$ such that

$$g_2'(x) = \frac{-g''(u_2 + x)x + g'(u_2 + x)}{x^2} = \frac{-g'''(\tilde{x})}{2} > 0, \tag{2.23}$$

which implies that $g_2(x)$ is strictly increasing. Then, for $x \in (u_1 - u_2, u^*)$ and $x \neq 0$,

$$\frac{|g'(u_2 + x)|}{|H_2(u_2 + x)|} = \frac{g_2(x)}{h_2(x)},$$

which is strictly increasing.

Step 2. We show that, for any $\xi \in (0, G_2(u^*))$, $g(\theta_2(-\xi)) > g(\theta_2(\xi))$. Noticing that $\theta_2(G_2(u)) = u$, we have $\theta_2'(\xi) = \dfrac{1}{|H_2(\theta_2(\xi))|}$ for $\xi \in (0, G_2(u^*))$, and consequently,

$$\begin{aligned} g(\theta_2(\xi)) =& g(\theta_2(0)) + \int_0^{\xi} \frac{g'(\theta_2(s))}{|H_2(\theta_2(s))|}\mathrm{d}s, \\ g(\theta_2(-\xi)) =& g(\theta_2(0)) + \int_0^{-\xi} \frac{g'(\theta_2(s))}{|H_2(\theta_2(s))|}\mathrm{d}s. \end{aligned} \tag{2.24}$$

It follows from Eq. (2.8) that $g'(\theta_2(s)) < 0$, and $g'(\theta_2(-s)) > 0$ for $\theta_2(-s) \in (u_1, u_2)$, and $g'(\theta_2(-s)) < 0$ for $\theta_2(-s) \in (0, u_1)$. Then, by virtue of Eq. (2.24), we have

$$\begin{aligned} g(\theta_2(-\xi)) - g(\theta_2(\xi)) &= \int_0^{-\xi} \frac{g'(\theta_2(s))}{|H_2(\theta_2(s))|}\mathrm{d}s - \int_0^{\xi} \frac{g'(\theta_2(s))}{|H_2(\theta_2(s))|}\mathrm{d}s \\ &= -\int_0^{\xi} \frac{g'(\theta_2(-s))}{|H_2(\theta_2(-s))|}\mathrm{d}s + \int_0^{\xi} \frac{|g'(\theta_2(s))|}{|H_2(\theta_2(s))|}\mathrm{d}s \\ &= -\int_0^{\xi} \frac{g'(u_2 + (\theta_2(-s) - u_2))}{|H_2(u_2 + (\theta_2(-s) - u_2))|}\mathrm{d}s + \int_0^{\xi} \frac{|g'(u_2 + (\theta_2(s) - u_2))|}{|H_2(u_2 + (\theta_2(s) - u_2))|}\mathrm{d}s. \end{aligned} \tag{2.25}$$

It follows from the results in Step 1 that, for $\theta_2(-s) \in (u_1, u_2)$,

$$\frac{g'(u_2 + (\theta_2(-s) - u_2))}{|H_2(u_2 + (\theta_2(-s) - u_2))|} = \frac{|g'(u_2 + (\theta_2(-s) - u_2))|}{|H_2(u_2 + (\theta_2(-s) - u_2))|} < \frac{|g'(u_2 + (\theta_2(s) - u_2))|}{|H_2(u_2 + (\theta_2(s) - u_2))|}.$$

Noticing that $g'(\theta_0(-s)) < 0$ for $\theta_2(-s) \in (0, u_1)$, we have

$$\frac{g'(u_2 + (\theta_2(-s) - u_2))}{|H_2(u_2 + (\theta_2(-s) - u_2))|} < \frac{|g'(u_2 + (\theta_2(s) - u_2))|}{|H_2(u_2 + (\theta_2(s) - u_2))|}$$

for $\theta_2(-s) \in (0, u_1)$. Therefore, $g(\theta_2(-\xi)) > g(\theta_2(\xi))$ for any $\xi \in (0, G_2(u^*))$.

Step 3. Finally, we show that $g(\theta(-\xi)) > g(\theta(\xi))$ for $\xi \in (0, \xi^*)$. By the arguments similar to Step 3 of Theorem 2.3, and replacing u_c, H_0, β_0 with u_2, H_2, β_2, we can easily obtain this result, and here we omit the proof. □

Then, by virtue of Theorems 2.2, 2.5 and the Poincaré-Bendixson theorem, we have the following results on the global dynamics of model (1.3) for $h = 2$.

Theorem 2.6. *Assume that $\beta, r, c, \theta > 0$, and $h = 2$. Then*

1. *if (u_-, v_-) is the unique positive equilibrium of system (1.3), and $g(u)$ satisfies (a_1) or satisfies (a_2) but $u_- > u_2$, then for any positive initial value (u_0, v_0), the corresponding solution of system (1.3) converges to (u_-, v_-).*
2. *if system (1.3) has two positive equilibria (u_-, v_-) and (u_+, v_+), $(u_- < u_+)$, and $g(u)$ satisfies (a_1) or satisfies (a_2) but $u_- \in (0, \overline{u}_1) \cup (u_2, 1)$, then (u_+, v_+) is a saddle point, and the stable manifold of (u_+, v_+) divides the first quadrant of $u - v$ plane into two subregions Ω_1 and Ω_2. The solutions with initial value in Ω_1 converge to (u_-, v_-), and that with initial value in Ω_2 converge to $(1, 0)$ as $t \to \infty$.*

We remark here for the case that $h = 2$ and $g(u)$ satisfies (a_2), (u_-, v_-) is locally stable when $u_- \in (0, u_1) \cup (u_2, 1)$ and unstable when $u \in (u_1, u_2)$. Theorem 2.4 shows that local stability of (u_-, v_-) implies global or bistable phenomenons for $u_- \in (0, \overline{u}_1) \cup (u_2, 1)$.

3. Numerical simulations and applications

In this subsection, we give some remarks on model (1.3). Firstly, we point out that if $\theta = 0$, then model has only one positive equilibrium. However, if $\theta \neq 0$, there may exist two positive equilibria, and bistable phenomenon can occur. Therefore, toxin effect can induce bistable phenomenon. Then, we remark that the dynamics of system (1.3) is complex if $g'(u_-) > 0$. We remark that the dynamics of system (1.3) is complex if $g'(u_-) > 0$. In this case, the ω limit set of a positive solution of system (1.3) can be equilibrium $(1, 0)$, a period orbit, or a homoclinic orbit, and there may exist periodic orbits or homoclinic orbits for system (1.3). For example, by virtue of Poincaré-Bendixson theorem, we have the following result when there exists a unique positive equilibrium.

Proposition 3.1. *Assume that (u_-, v_-) is the unique positive equilibrium of system (1.3) and $g'(u_-) > 0$. Then (u_-, v_-) is unstable, and system (1.3) has at least one periodic orbit.*

Bifurcations such as Hopf bifurcation and homoclinic bifurcation all await future investigation. Finally, we give some numerical simulations to show the stable and bistable phenomenons for model (1.3). Let

$$h = 1, \quad r = 2, \quad \theta = 2, \quad c = 2,$$

and β be the variable parameter. By virtue of Theorems 2.1, 2.4 and Proposition 3.1, we have the following results, (see also Fig. 1).

(a) If $\beta \in (0, 11.6569)$, then for any positive initial value (u_0, v_0), the corresponding solution of system (1.3) converges to $(1, 0)$.

(b) If $\beta \in (11.6569, 12)$, then there exists bistable phenomenon. The stable manifold of (u_+, v_+) divides the first quadrant of $u - v$ plane into two subregions Ω_1 and Ω_2. The solutions with initial value in Ω_1 converge to (u_-, v_-), and that with initial value in Ω_2 converge to $(1, 0)$ as $t \to \infty$.

(c) If $\beta \in (12, 15)$, then for any positive initial value (u_0, v_0), the corresponding solution of system (1.3) converges to (u_-, v_-).

(d) If $\beta \in (15, \infty)$, then (u_-, v_-) is unstable, and system (1.3) has at least one periodic orbit.

Finally, we show some applications of the obtained results. We revisit the following toxic phytoplankton-zooplankton model with delay:

$$\begin{cases} \dfrac{\mathrm{d}P}{\mathrm{d}t} = bP\left(1 - \dfrac{P}{k}\right) - \dfrac{\alpha PZ}{1 + cP}, & t > 0, \\ \dfrac{\mathrm{d}Z}{\mathrm{d}t} = \dfrac{\beta PZ}{1 + cP} - rZ - \theta P(t - \tau)Z, & t > 0, \\ P(0) = P_0 \geq 0, \quad Z(0) = Z_0 \geq 0. \end{cases} \tag{3.1}$$

In [23], Wang et al. showed that under certain conditions, there exist two sequences $\{\tau_j^+\}_{j=0}^{\infty}$ and $\{\tau_j^-\}_{j=0}^{\infty}$ such that model (3.1) occurs Hopf bifurcation when $\tau = \tau_j^+$ or $\tau = \tau_j^-$. Our results in this paper imply that there exist no periodic solutions for system (1.3) when (u_-, v_-) is locally asymptotically stable, which implies that system (3.1) has no periodic solutions with period τ under the above condition.

Then we can improve the local Hopf bifurcation results in [23] and obtain the global bifurcation results for Hopf bifurcation points $\{\tau_j^+\}_{j=1}^{\infty}$ and $\{\tau_j^-\}_{j=1}^{\infty}$. Here we omit the details.

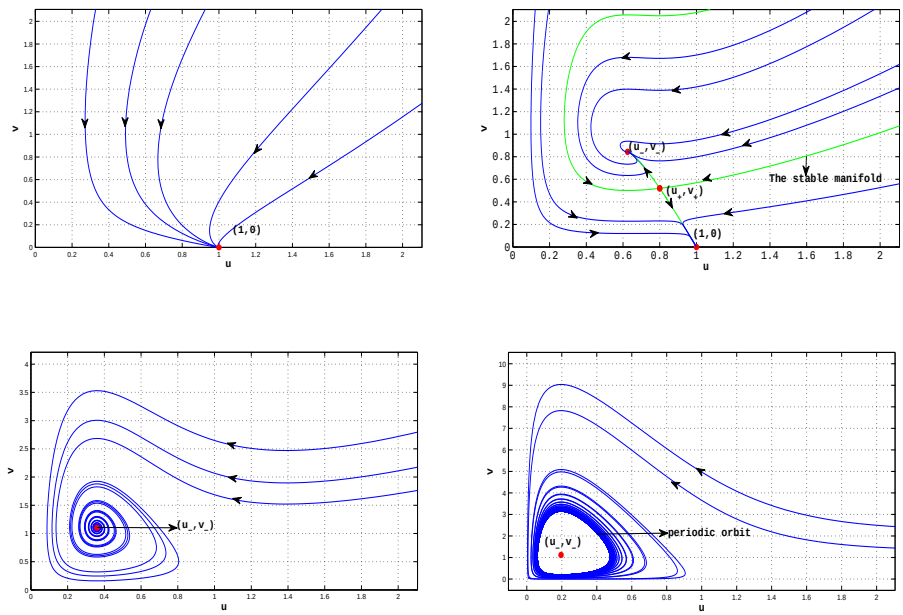

Figure 1. Phase portraits for system (1.3). (Upper left) Here $\beta = 9$, and $(1, 0)$ is globally attractive; (Upper right) Here $\beta = 11.7$, and bistable phenomenon occurs; (Lower left) Here $\beta = 13$, and (u_-, v_-) is globally attractive; (Lower right) Here $\beta = 17$, and there exists a periodic orbit.

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