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TIME-DELAYED MODELS FOR THE EFFECTS OF TOXICANTS ON POPULATIONS IN CONTAMINATED AQUATIC ECOSYSTEMS

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ABSTRACT. Ecotoxicological models play a vital role in understanding the influence of toxicants on population dynamics in contaminated aquatic ecosystems. Traditional differential equation models describing interactions between populations and toxicants typically assume instantaneous population growth, overlooking potential time delays associated with reproductive and maturation processes. In this paper, we introduce two models with time delays to investigate the interaction between a population and a toxicant, where the population growth is governed by a delayed logistic equation. We mainly focus on the stability analysis of the steady states of the models. Our findings indicate that high toxicant concentrations result in population extinction, whereas moderate toxicant levels can potentially induce bistability, where the population's fate, whether persistence or extinction, depends on the initial densities of the population and toxicant. Furthermore, both our theoretical analysis and numerical simulations demonstrate that the time delay can lead to the destabilization of the coexistence steady states and the appearance of periodic solutions through Hopf bifurcation.

1. INTRODUCTION

Chemical pollutants are extensively spread across Earth's ecosystems due to a variety of human activities and natural occurrences, with the potential to harm a wide array of organisms [24]. Toxic substances in aquatic environments can present a danger to every tier of the biological structure, from individual organisms to populations, communities, and entire ecosystems [1, 19]. By conducting risk assessments, numerous water quality standards and efficient control methods have been suggested to prevent species loss and preserve ecosystem functions [3, 4, 6, 11, 20, 25, 26]. Accurate assessment of the risks associated with toxic substances requires more than just comprehension of their effects on individual organisms, but necessitates further grasp of population dynamics and complex ecological interactions.

Mathematical models have become a potent tool for investigating and enhancing our understanding of how toxicants affect population dynamics in ecological systems. In particular, a large number of differential equation models have been developed to describe the nonlinear dynamic nature of interactions between populations and toxicants in contaminated aquatic ecosystems (see, e.g.,[7, 8, 9, 10, 12, 13, 16, 17, 22]). It is worth noticing that the aforementioned differential equation models assume that populations undergo logistic growth, where the growth is assumed to act instantly, whereas there may be a time delay to account for the time to maturity, the finite gestation period, and other factors [21]. In this work, we study the following delayed differential equation (DDE) model for the interaction

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between a population and a toxicant:

$$\begin{cases} \frac{\mathrm{d}u(t)}{\mathrm{d}t} = ru(t)\left[1 - \frac{u(t-\tau)}{K}\right] - mw(t)u(t), \\ \frac{\mathrm{d}w(t)}{\mathrm{d}t} = h - pu(t)w(t) - qw(t), \\ u(\theta) = u_0(\theta) \geq\not\equiv 0, w(0) = w_0 \geq 0,\ \theta \in [-\tau, 0]. \end{cases} \tag{1.1}$$

where $u(t)$ represents the population density at time t, $w(t)$ denotes the toxicant concentration at time t. The model parameters r, K, m, h, p, q are all positive constants. The first equation of (1.1) describes the population growth under the influence of the toxicant. The term $ru(t)[1 - u(t-\tau)/K]$ is commonly known as the delayed logistic growth, proposed by Hutchinson [14], where r is the intrinsic growth rate, K is the carrying capacity of the environment, the delay τ may represents the maturation time of the individuals in the population [18] or the recovery time of environmental resources after they have been consumed by the population [21]. The term $mw(t)u(t)$ describes the negative effects of the toxicant on the population growth, which is assumed to be proportional to the toxicant concentration, where m is the effect coefficient. The second equation of (1.1) is a balance equation for the toxicant concentration. The parameter h is the input rate at which exogenous toxicant into the environment. The term puw is the rate at which the population takes up the toxicant, which is modeled in terms of the mass action law hence is proportional to both the toxicant concentration and the population density. The parameter q represents the unit output rate of toxicant because of a variety of factors, such as environmental detoxification, microbial degradation, and so on. The last line of (1.1) gives the initial conditions.

The DDE model (1.1) ignores the spatial dispersal of the population and the toxicant. However, both the population and the toxicant may spread spatially due to active mobility or passive diffusion driven by turbulent water. This motivates us to extend the DDE model (1.1) to the following reaction-diffusion equation (RDE) model:

$$\begin{cases} \partial_t u(x,t) = d_1 \partial_{xx} u(x,t) + ru(x,t)\left[1 - \frac{u(x,t-\tau)}{K}\right] - mw(x,t)u(x,t), x \in (0, l\pi), t > 0, \\ \partial_t w(x,t) = d_2 \partial_{xx} w(x,t) + h - pu(x,t)w(x,t) - qw(x,t),\ x \in (0, l\pi), t > 0, \\ \partial_x u(0,t) = \partial_x w(0,t) = 0, u_x(l\pi, t) = w_x(l\pi, t) = 0,\ t > 0, \\ u(x,\theta) = u_0(x,\theta) \geq\not\equiv 0, w(x,0) = w_0(x) \geq\not\equiv 0,\ x \in [0, l\pi], \theta \in [-\tau, 0], \end{cases} \tag{1.2}$$

where $u(x,t)$ represents the population density at location x and time t, $w(x,t)$ denotes the toxicant concentration at location x and time t, d_1 and d_2 are diffusion coefficients, l is a positive integer.

The main goal of this work is to investigate how the interplay among the toxicant input rate h, the time delay τ, and other model parameters affect the population persistence. To this end, we organize the rest of the paper as follows. In the next section, we analyze the existence and stability of the equilibria of the DDE system (1.1). In section 3, we examine the stability of the spatially homogeneous steady states of the RDE system (1.2). In section 4, we make numerical simulations to validate the theoretical results. Finally, in section 5, we remark the conclusions and limitations of the current work and suggest future research directions.

2. Stability analysis of the DDE system (1.1)

When $\tau = 0$, the DDE system (1.1) reduces to the ordinary differential equation (ODE) system

$$\begin{cases} \frac{\mathrm{d}u(t)}{\mathrm{d}t} = ru(t)\left[1 - \frac{u(t)}{K}\right] - mw(t)u(t), \\ \frac{\mathrm{d}w(t)}{\mathrm{d}t} = h - pu(t)w(t) - qw(t), \\ u(0) = u_0 > 0, w(0) = w_0 > 0. \end{cases} \tag{2.1}$$

The existence and stability of the equilibria of the ODE system (2.1) have been discussed in [5].

For notational convenience, we let

$$h_1 =: \frac{qr}{m}, \quad h_2 =: \frac{(Kp+q)^2 r}{4Kpm}.$$

System (2.1) has the following three possible equilibria:

$$(0, \bar{w}) = (0, \frac{h}{q}),$$

$$(u_*, w_*) = \left(\frac{Kpr - qr + \sqrt{\triangle}}{2pr}, \frac{h}{pu_* + q} \right),$$

$$(u^*, w^*) = \left(\frac{Kpr - qr - \sqrt{\triangle}}{2pr}, \frac{h}{pu^* + q} \right),$$

where $\triangle = (Kp+q)^2 r^2 - 4Kprmh \geq 0$, which is equivalent to $h \leq h_2$. The toxicant-only equilibrium $(0, \bar{w})$ (at which the population goes extinct) always exists, while the coexistence equilibria (u_*, w_*) and (u^*, w^*) exist under certain conditions.

We summarize the conditions on the existence and stability of the equilibria of system (2.1) in Table 1. See [5] for more detailed discussion.

TABLE 1. The existence of the equilibria and the asymptotic dynamics of system (2.1). Where LAS represents locally asymptotically stable, GAS represents globally asymptotically stable, US represents unstable, TB represents transcritical bifurcation, S-NB represents saddle-node bifurcation. Note that $p = \frac{q}{K} \Leftrightarrow h_1 = h_2$.

<table>
<tr><th></th><th>$h < h_1$</th><th>$h = h_1$</th><th>$h_1 < h < h_2$</th><th>$h = h_2$</th><th>$h > h_2$</th></tr>
<tr><td>$p > \frac{q}{K}$</td><td rowspan="3">$(0, \bar{w})$: US
(u_*, w_*): GAS</td><td>$(0, \bar{w})$: TB
(u_*, w_*): LAS</td><td>$(0, \bar{w})$: LAS
(u_*, w_*): LAS
(u^*, w^*): US</td><td>$(0, \bar{w})$: LAS
$(u_*, w_*) =$
(u^*, w^*): S-NB</td><td rowspan="3">$(0, \bar{w})$: GAS</td></tr>
<tr><td>$p = \frac{q}{K}$</td><td rowspan="2">$(0, \bar{w})$: TB</td><td>not applicable</td><td>$(0, \bar{w})$: TB</td></tr>
<tr><td>$p < \frac{q}{K}$</td><td>$(0, \bar{w})$: GAS</td><td>$(0, \bar{w})$: GAS</td></tr>
</table>

Since the DDE system (1.1) has the same equilibria as the ODE system (2.1), in what follows, we discuss the effects of the time delay τ on the stability of the equilibria of system (1.1). For $\tau > 0$, it is well known that an equilibrium (u_s, w_s) of system (1.1) is asymptotically stable if the zero equilibrium $(0, 0)$ of the linearized system at (u_s, w_s) is asymptotically stable. Let $U(t) = u(t) - u_s, W(t) = w(t) - w_s$. Then the linearized system of (1.1) at (u_s, w_s), which can be one of $(0, \bar{w})$,(u_*, w_*), and (u^*, w^*), is

$$\begin{cases} \frac{\mathrm{d}U(t)}{\mathrm{d}t} = (r - mw_s - \frac{r}{K}u_s)U(t) - mu_s W(t) - \frac{r}{K}u_s U(t-\tau), \\ \frac{\mathrm{d}W(t)}{\mathrm{d}t} = -pw_s U(t) - (pu_s + q)W(t). \end{cases} \tag{2.2}$$

In order to obtain the characteristic equation of (2.2), we assume

$$U(t) = u_0 e^{\lambda t}, W(t) = w_0 e^{\lambda t}, u_0 \neq 0, w_0 \neq 0,$$

is an exponential solution of system (2.2). Substituting it into (2.2), we obtain

$$\begin{aligned}\lambda \begin{bmatrix} u_0 \\ w_0 \end{bmatrix} e^{\lambda t} &= \begin{bmatrix} (r - mw_s - \frac{r}{K}u_s)u_0e^{\lambda t} - mu_sw_0e^{\lambda t} - \frac{r}{K}u_su_0e^{\lambda(t-\tau)} \\ -pw_su_0e^{\lambda t} - (pu_s+q)w_0e^{\lambda t} \end{bmatrix} \\ &= (A + Be^{-\lambda\tau}) \begin{bmatrix} u_0 \\ w_0 \end{bmatrix} e^{\lambda t},\end{aligned}$$

where

$$A = \begin{bmatrix} r - mw_s - \frac{r}{K}u_s & -mu_s \\ -pw_s & -(pu_s+q) \end{bmatrix}, \quad B = \begin{bmatrix} -\frac{r}{K}u_s & 0 \\ 0 & 0 \end{bmatrix}.$$

Since $u_0 \neq 0, w_0 \neq 0$, $e^{\lambda t} \neq 0$, we can get the following characteristic equation

$$\mathrm{Det}(A + Be^{-\lambda\tau} - \lambda I) = 0,$$

which is equivalent to the transcendental equation

$$\lambda^2 + P\lambda + R + (S\lambda + Q)e^{-\lambda\tau} = 0, \tag{2.3}$$

where

$$\begin{aligned}&P = pu_s + q - (r - mw_s - \tfrac{r}{K}u_s),\ R = -mpu_sw_s - (r - mw_s - \tfrac{r}{K}u_s)(pu_s+q),\\ &S = \tfrac{r}{K}u_s,\ Q = \tfrac{r}{K}u_s(pu_s+q).\end{aligned}$$

For the toxicant-only equilibrium $(0,\bar{w})$, $P = q - r + \frac{mh}{q}$, $R = -q(r - \frac{mh}{q})$, $Q = S = 0$. Hence the characteristic equation corresponding to $(0,\bar{w})$ is

$$\lambda^2 + \left(q - r + \frac{mh}{q}\right)\lambda - q\left(r - \frac{mh}{q}\right) = 0,$$

which has two real roots $\lambda_1 = -q < 0$, $\lambda_2 = r - \frac{hm}{q}$. Thus, we have

Theorem 2.1. *The following statements hold.*

(i) *If $h > h_1$, then the toxicant-only equilibrium $(0,\bar{w})$ is absolutely stable, that is, $(0,\bar{w})$ is locally asymptotically stable for any $\tau > 0$.*

(ii) *If $h < h_1$, then for any $\tau > 0$, the toxicant-only equilibrium $(0,\bar{w})$ is always unstable.*

For the coexistence equilibrium (u_*, w_*) satisfying $r(1 - \frac{u_*}{K}) - mw_* = 0$ and $pu_*w_* + qw_* = h$, the coefficients of the characteristic equation (2.3) are

$$P = pu_* + q,\ R = -mpu_*w_*,\ S = \frac{r}{K}u_*,\ Q = PS. \tag{2.4}$$

Thus,

$$\begin{aligned}R^2 - Q^2 &= (mpu_*w_*)^2 - \frac{r^2}{K^2}(pu_*+q)^2(u_*)^2 \\ &= \left[mpu_*\frac{r(K-u_*)}{Km}\right]^2 - \frac{r^2}{K^2}(pu_*+q)^2(u_*)^2 \\ &= \frac{r^2}{K^2}(u_*)^2(Kp+q)(Kp-q-2pu_*). \\ &= -\frac{r}{K^2}{u_*}^2\,(Kp+q)\,\sqrt{\triangle} < 0.\end{aligned}$$

For the coexistence equilibrium (u^*, w^*), similar calculations give that $R^2 - Q^2 > 0$. Thus, $R^2 - Q^2 \neq 0$ holds at both coexistence equilibria, which implies that $\lambda = 0$ cannot be the root of the characteristic equation (2.3).

Next, we analyze the existence of purely imaginary roots of (2.3). We assume that the characteristic equation (2.3) has a purely imaginary root $i\omega, \omega > 0$, substituting $\lambda = i\omega$ into (2.3), we get

$$-\omega^2 + R + S\omega\sin(\omega\tau) + Q\cos(\omega\tau) + [P\omega + S\omega\cos(\omega\tau) - Q\sin(\omega\tau)]i = 0.$$

Separating the real part and imaginary part, we obtain

$$\begin{cases} -\omega^2 + R = -S\omega\sin(\omega\tau) - Q\cos(\omega\tau), \\ P\omega = -S\omega\cos(\omega\tau) + Q\sin(\omega\tau), \end{cases} \tag{2.5}$$

therefore ω satisfies

$$\omega^4 - (S^2 - P^2 + 2R)\omega^2 + (R^2 - Q^2) = 0. \tag{2.6}$$

If $(S^2 - P^2 + 2R)^2 - 4(R^2 - Q^2) \geq 0$, we can solve (2.6) for ω^2 to get

$$\omega_\pm^2 = \frac{S^2 - P^2 + 2R \pm \sqrt{(S^2 - P^2 + 2R)^2 - 4(R^2 - Q^2)}}{2}. \tag{2.7}$$

On the other hand, from (2.5), we can also deduce that

$$\sin\left(\omega_\pm \tau_j^\pm\right) = \frac{(PQ - RS)\omega_\pm + S\omega_\pm^3}{Q^2 + S^2\omega_\pm^2}.$$

Noticing that the coefficients of the characteristic equation corresponding to coexistence equilibria (u_*, w_*) and (u^*, w^*) satisfy $P > 0, R < 0, S > 0, Q = PS > 0$ (see (2.4)), we conclude that $\sin\left(\omega_\pm \tau_j^\pm\right) > 0$. Moreover, if $i\omega_\pm$ are the roots of the characteristic equation (2.3), the corresponding delay values are

$$\begin{aligned} \tau_j^\pm &= \frac{1}{\omega_\pm}\arccos\left\{\frac{(Q - PS)\omega_\pm^2 - QR}{S^2\omega_\pm^2 + Q^2}\right\} + \frac{2j\pi}{\omega_\pm} \\ &= \frac{1}{\omega_\pm}\arccos\left\{\frac{-QR}{S^2\omega_\pm^2 + Q^2}\right\} + \frac{2j\pi}{\omega_\pm}, \quad j = 0, 1, 2... \end{aligned} \tag{2.8}$$

If $\lambda_j^\pm = \alpha_j^\pm(\tau) + i\beta_j^\pm(\tau), \alpha_j^\pm(\tau_j^\pm) = 0, \beta_j^\pm(\tau_j^\pm) = \omega_\pm, j = 0, 1, 2\ldots$, are the roots of (2.3), then we are able to show that the following transversality conditions hold.

Lemma 2.2. *The following statements hold.*

- (i) *If $R^2 - Q^2 < 0$ holds for some n, then the characteristic equation* (2.3) *has a purely imaginary root $i\omega^+$, it satisfies $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\{\lambda_j^+(\tau_j^+)\} > 0$.*
- (ii) *If $R^2 - Q^2 > 0$ and $S^2 - P^2 + 2R > 0$ hold for some n,*
  - (a) *if $(S^2 - P^2 + 2R)^2 - 4(R^2 - Q^2) > 0$, then the characteristic equation* (2.3) *has two purely imaginary roots $i\omega^+$ and $i\omega^-$, they satisfy $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\{\lambda_j^+(\tau_j^+)\} > 0$, $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\{\lambda_j^-(\tau_j^-)\} < 0$;*
  - (b) *if $(S^2 - P^2 + 2R)^2 - 4(R^2 - Q^2) = 0$, then the characteristic equation* (2.3) *has a purely imaginary root $i\omega^+ = i\omega^-$, it satisfies $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\{\lambda_j^\pm(\tau_j^\pm)\} = 0$;*
  - (c) *if $(S^2 - P^2 + 2R)^2 - 4(R^2 - Q^2) < 0$, then the characteristic equation* (2.3) *has no purely imaginary root.*
- (iii) *If $R^2 - Q^2 > 0$ and $S^2 - P^2 + 2R \leq 0$ hold for some n, then the characteristic equation* (2.3) *has no purely imaginary root.*

Proof. The distribution of the roots of characteristic equation (2.3) can be obtained by analysing equation (2.6), here we mainly discuss the transversality conditions. Differentiating (2.3) with respect to τ, we have

$$\left(2\lambda + P + [S - \tau(S\lambda + Q)]e^{-\lambda\tau}\right)\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} = \lambda(S\lambda + Q)e^{-\lambda\tau},$$

which gives that

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{(2\lambda + P)e^{\lambda\tau} + S}{\lambda(S\lambda + Q)} - \frac{\tau}{\lambda}.$$

From (2.3), we see that

$$e^{\lambda\tau} = -\frac{S\lambda + Q}{\lambda^2 + P\lambda + R}.$$

Therefore,

$$\begin{aligned}
\text{sign}\left\{\frac{\mathrm{d}(\mathrm{Re}\lambda)}{\mathrm{d}\tau}\right\}_{\lambda=i\omega_\pm} &= \text{sign}\left\{\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\right\}_{\lambda=i\omega\pm} \\
&= \text{sign}\left\{\mathrm{Re}\left[-\frac{2\lambda + P}{\lambda(\lambda^2 + P\lambda + R)}\right]_{\lambda=i\omega_\pm} + \mathrm{Re}\left[\frac{S}{\lambda(S\lambda + Q)}\right]_{\lambda=i\omega_\pm}\right\} \\
&= \text{sign}\left\{\frac{P^2 - 2(R - \omega_\pm^2)}{(R - \omega_\pm^2)^2 + P^2\omega_\pm^2} + \frac{-S^2}{S^2\omega_\pm^2 + Q^2}\right\} \\
&= \text{sign}\left\{P^2 - 2(R - \omega_\pm^2) - S^2\right\} \\
&= \text{sign}\left\{\pm\sqrt{(S^2 - P^2 + 2R)^2 - 4(R^2 - Q^2)}\right\},
\end{aligned}$$

The lemma is proved. □

Based on previous discussion and Lemma 2.2, we can get the stability conclusion of system (1.1) at the equilibrium (u_*, w_*) as follows.

Theorem 2.3. *If $h < h_2$, then (u_*, w_*) is conditionally stable, that is, there exists τ_0^+ given by (2.8) such that*

(i) *when $\tau \in [0, \tau_0^+)$, (u_*, w_*) is locally asymptotically stable;*
(ii) *when $\tau = \tau_0^+$, a Hopf bifurcation is generated at (u_*, w_*);*
(iii) *when $\tau > \tau_0^+$, (u_*, w_*) is unstable.*

Proof. From the previous analysis, we know that for the coexistence equilibrium (u_*, w_*), $R^2 - Q^2 < 0$. Hence from Lemma 2.2, we can see that when $\tau = \tau_j^+$, the characteristic equation (2.3) has a pair of purely imaginary roots $\pm i\omega_+$.

According to Table 1, when $\tau = 0$ and $h < h_2$, (u_*, w_*) is stable as long as it exists. When $\tau = \tau_0^+$, the characteristic equation (2.3) has a pair of purely imaginary roots $\pm i\omega_+$ for the first time and they satisfy the transversal condition in Lemma 2.2. Refer to Theorem 1.4 in [15], we can deduce that if $\tau \in [0, \tau_0^+)$, (u_*, w_*) is locally asymptotically stable; if $\tau = \tau_0^+$, a Hopf bifurcation is generated at (u_*, w_*); if $\tau > \tau_0^+$, (u_*, w_*) will lose its stability and never acquire it again. The theorem is proved. □

Regarding the coexistence equilibrium (u^*, w^*), we have the result below.

Theorem 2.4. *If $h_1 < h < h_2$, then (u^*, w^*) is unstable for any $\tau > 0$.*

Proof. We divide the proof into the following three cases.

Case I. The characteristic equation (2.3) has no purely imaginary root for any $\tau > 0$. For this case, since (u^*, w^*) is unstable in system (1.1) when $\tau = 0$, so (u^*, w^*) is unstable for any $\tau > 0$.

Case II. When $\tau = \tau_j^+$, (2.3) has a pair of imaginary roots $\pm i\omega_+$. For this case, based on the fact that (u^*, w^*) is unstable in system (1.1) when $\tau = 0$ and the transversal conditions in Lemma 2.2, we conclude that (u^*, w^*) is unstable for any $\tau > 0$.

Case III. When $\tau = \tau_j^{\pm}$, (2.3) has two pairs of purely imaginary roots $\pm i\omega_+$ and $\pm i\omega_-$. From (2.8) we can get

$$\tau_0^{\pm} = \frac{1}{\omega_{\pm}} \arccos\left\{\frac{-QR}{S^2\omega_{\pm}^2 + Q^2}\right\},$$

since $\omega_+ > \omega_-$ and $\arccos(\cdot)$ is a monotonically decreasing function, so $\tau_0^+ < \tau_0^-$. Note that

$$\tau_{j+1}^+ - \tau_j^+ = \frac{2j\pi}{\omega_+} < \frac{2j\pi}{\omega_-} = \tau_{j+1}^- - \tau_j^-.$$

Therefore, as j increases, there exists a positive integer k such that the sequence $\{\tau_j^{\pm}\}$ satisfies

$$\tau_0^+ < \tau_0^- < \tau_1^+ < \cdots < \tau_{k-1}^+ < \tau_{k-1}^- < \tau_k^+ < \tau_{k+1}^+ < \tau_k^- \cdots.$$

According to the transversal conditions in Lemma (2.2), it follows that as τ passes τ_j^+, there is a pair of characteristic roots crossing from the left half plane of the complex plane to the right half plane, and as τ passes τ_j^-, there is a pair of characteristic roots crossing from the right half plane to the left half plane. Consequently, combining the fact that (u^*, w^*) is unstable when $\tau = 0$, we can deduce that for any $\tau > 0$, there is always a root in the right half plane. In other words, the characteristic equation (2.3) always has a root with real part greater than zero. Therefore, (u^*, w^*) is unstable for any $\tau > 0$. □

3. Linear stability analysis of the RDE system (1.2)

3.1. **Stability analysis at** $(0, \bar{w})$**.** In this part, we will study the stability of model (1.2) by analyzing its characteristic equation at extinction equilibrium $(0, \bar{w})$. Let $U(x,t) = u(x,t), W(x,t) = w(x,t) - \bar{w}$. Then the linearized system of (1.2) at $(0, \bar{w})$ is

$$\begin{cases} \partial_t U(x,t) = d_1 \partial_{xx} U(x,t) + \left(r - \frac{hm}{q}\right) U(x,t), \\ \partial_t W(x,t) = d_2 \partial_{xx} W(x,t) - p\frac{h}{q} U(x,t) - qW(x,t). \end{cases} \tag{3.1}$$

Let

$$\Psi(x,t) = \begin{bmatrix} U(x,t) \\ W(x,t) \end{bmatrix}, \ D = \begin{bmatrix} d_1 & \\ & d_2 \end{bmatrix}, \ J = \begin{bmatrix} r - \frac{hm}{q} & 0 \\ -p\frac{h}{q} & -q \end{bmatrix}.$$

Then system (3.1) can be expressed as

$$\Psi_t(x,t) = D\partial_{xx}\Psi(x,t) + J\Psi(x,t). \tag{3.2}$$

It is well known that the eigenvalues of the differentiation operator $-\partial_{xx}$ on $[0, l\pi]$ subject to Neumann boundary condition are $\lambda_n = n^2/l^2$ $(n = 0, 1, 2, \cdots)$. Let $\varphi_n(x)$ be the eigenfunctions corresponding to λ_n. We then look for solutions of (3.2) of the form

$$\Psi_n(x,t) = c\varphi_n(x)e^{\rho t}, \tag{3.3}$$

where c is a two-dimensional constant column vector, ρ is a temporal eigenvalue. According to the superposition principle, the linear system (3.2) has the solution

$$\Psi(x,t) = \sum_{n=0}^{\infty} \Psi_n(x,t).$$

Substituting (3.3) into (3.2), we have

$$\rho c = \left(-\frac{n^2}{l^2}D + J\right)c,$$

which implies that ρ is the eigenvalue of the matrix

$$M_n := -\frac{n^2}{l^2}D + J = \begin{bmatrix} -d_1\frac{n^2}{l^2} + r - \frac{hm}{q} & 0 \\ -p\frac{h}{q} & -d_2\frac{n^2}{l^2} - q \end{bmatrix}.$$

If the toxicant-only equilibrium $(0, \bar{w})$ is locally asymptotically stable in the ODE system (2.1) (from Theorem 2.1, it is also locally asymptotically stable in the DDE system (1.1)), then $h > h_1$ (see Table 1) and $-d_1n^2/l^2 + r - hm/q < 0$, which indicates that

$$\text{Trace}\,(M_n) < 0,\ \text{Det}\,(M_n) > 0,$$

therefore all eigenvalues of M_n have a negative real part. Thus, we have the following conclusion.

Theorem 3.1. *If $h > h_1$, then for any $\tau > 0$, the toxicant-only equilibrium $(0, \bar{w})$ is locally asymptotically stable in the delayed reaction-diffusion system (1.2).*

3.2. **Stability analysis at (u_*, w_*) and (u^*, w^*).** In this part, we will study the stability of model (1.2) by analyzing its characteristic equation at coexistence equilibrium (u_*, w_*). Let $U(x,t) = u(x,t) - u_*, W(x,t) = w(x,t) - w_*$. Then linearizing system (1.2) at (u_*, w_*) yields

$$\begin{cases} \partial_t U(x,t) = d_1\partial_{xx}U(x,t) - mu_*W(x,t) - \frac{r}{K}u_*U(x,t-\tau), \\ \partial_t W(x,t) = d_2\partial_{xx}W(x,t) - pw_*U(x,t) - (pu_* + q)\,W(x,t). \end{cases} \tag{3.4}$$

Let state space $\mathcal{C} = C\left([0, l\pi] \times [-\tau, 0], \mathbb{R}^2\right)$, $\Psi(x,t) = (U(x,t), W(x,t))^T$, then system (3.4) can be expressed as an abstract differential equation in the phase space $\mathcal{C}$, namely,

$$\partial_t\Psi(x,t) = D\partial_{xx}\Psi(x,t) + L(\Psi_t), \tag{3.5}$$

where $D = \text{diag}(d_1, d_2), \Psi_t(x,\theta) = \Psi(x, t+\theta), x \in [0, l\pi], \theta \in [-\tau, 0]$, and $L : \mathcal{C} \longrightarrow \mathbb{R}^2$ is defined as

$$L(\varphi) = \begin{bmatrix} -\frac{r}{K}u_*\varphi_1(x,-\tau) - mu_*\varphi_2(x,0) \\ -pw_*\varphi_1(x,0) - (pu_* + q)\varphi_2(x,0) \end{bmatrix},$$

where $\varphi = (\varphi_1, \varphi_2)^T \in \mathcal{C}$.

Let $X = C\left([0, l\pi], \mathbb{R}^2\right)$, the characteristic equation of (3.5) is

$$\lambda y - D\partial_{xx}y - L(e^{\lambda\cdot}y) = 0, \tag{3.6}$$

where $y \in \text{Dom}(\partial_{xx}) - \{0\}$, and

$$\left(e^{\lambda\cdot}y\right)(x,\theta) = e^{\lambda\theta}y(x), -\tau \le \theta \le 0.$$

We know that the eigenvalues of $D\partial_{xx}$ on X subject to Neumann boundary condition are $-d_1n^2/l^2$ and $-d_2n^2/l^2, n = 0, 1, 2, \cdots$, and the corresponding eigenfunctions are

$$\beta_n^1 = \begin{bmatrix} \cos\left(\frac{nx}{l}\right) \\ 0 \end{bmatrix}, \beta_n^2 = \begin{bmatrix} 0 \\ \cos\left(\frac{nx}{l}\right) \end{bmatrix}, n = 0, 1, 2, \cdots,$$

which form a basis in the space X. Thus for any $y \in X$, it can be expressed as

$$y = \sum_{n=0}^{\infty} y_{1n}\beta_n^1 + y_{2n}\beta_n^2 = \sum_{n=0}^{\infty} \cos\left(\frac{nx}{l}\right) \begin{bmatrix} y_{1n} \\ y_{2n} \end{bmatrix}. \tag{3.7}$$

Inserting (3.7) into (3.6), we have

$$\sum_{n=0}^{\infty} \cos\left(\frac{nx}{l}\right) \left(\lambda I + \frac{n^2}{l^2}D + \begin{bmatrix} \frac{r}{K}u_*e^{-\lambda\tau} & mu_* \\ pw_* & (pu_* + q) \end{bmatrix}\right) \begin{bmatrix} y_{1n} \\ y_{2n} \end{bmatrix} = 0.$$

Hence (3.6) is equivalent to

$$\text{Det}\left(\lambda I + \frac{n^2}{l^2}D + \begin{bmatrix} \frac{r}{K}u_* e^{-\lambda\tau} & mu_* \\ pw_* & (pu_*+q) \end{bmatrix}\right) = 0,\ n = 0, 1, 2, \cdots,$$

that is,

$$\lambda^2 + A_n\lambda + B_n + (C_n\lambda + D_n)e^{-\lambda\tau} = 0,\ n = 0, 1, 2, \cdots, \tag{3.8}$$

where

$$A_n = (d_1+d_2)\tfrac{n^2}{l^2} + pu_* + q,\ B_n = d_1 d_2 \tfrac{n^4}{l^4} + d_1(pu_*+q)\tfrac{n^2}{l^2} - mpu_*w_*,$$
$$C_n = \tfrac{r}{K}u_*,\ D_n = \tfrac{d_2 r u_*}{K}\tfrac{n^2}{l^2} + \tfrac{r}{K}u_*(pu_*+q).$$

Next, we perform linear stability analysis for the case of $\tau = 0$ to determine whether pattern formation occurs at its spatial homogeneous equilibrium (u_*, w_*). When $\tau = 0$, the characteristic equation (3.8) reduces to

$$\lambda^2 + (A_n + C_n)\lambda + B_n + D_n = 0,\ n = 0, 1, 2, \cdots. \tag{3.9}$$

Denoting the nth characteristic roots as $\lambda_{1n}, \lambda_{2n}$, we obeserve that

$$\lambda_{1n} + \lambda_{2n} = -(A_n + C_n) = -(d_1+d_2)\frac{n^2}{l^2} - \frac{r}{K}u_* - pu_* - q < 0,$$

$$\lambda_{1n}\cdot\lambda_{2n} = B_n + D_n = d_1 d_2\frac{n^4}{l^4} + (d_1 pu_* + d_1 q + \frac{d_2 r}{K}u_*)\frac{n^2}{l^2} + \frac{pr}{K}{u_*}^2 + \frac{qr}{K}u_* - mpu_*w_*.$$

Note that when $n = 0$, equation (3.9) is the characteristic equation of the ODE system (2.1) at the equilibrium (u_*, w_*) and $\lambda_{10}, \lambda_{20}$ are the corresponding roots. If $h < h_2$, then (u_*, w_*) is locally asymptotically stable in (2.1), which means that

$$\lambda_{10}\cdot\lambda_{20} = \frac{pr}{K}{u_*}^2 + \frac{qr}{K}u_* - mpu_*w_* > 0,$$

combining with

$$d_1 pu_* + d_1 q + \frac{d_2 r}{K}u_* > 0,$$

we can get $\lambda_{1n}\cdot\lambda_{2n} = B_n + D_n > 0$, therefore when $\tau = 0$, (u_*, w_*) is linearly stable in system (1.2). This can be expressed as the following theorem.

Theorem 3.2. *If $h < h_2$, then when $\tau = 0$, the coexistence equilibrium (u_*, w_*) is linearly stable (no pattern formation occurs) in the reaction-diffusion system (1.2).*

We now study the effect of the delay on system (1.2) by analyzing characteristic equation (3.8). If for any positive integer n, all the roots of (3.8) have negative real parts, then (u_*, w_*) is linearly stable. However, if there exists some integer n such that (3.8) has a root whose real part is greater than zero, then (u_*, w_*) is unstable.

Since $B_n + D_n > 0$, so zero is not a root of (3.8). According to Theorem 1.4 of [15], we only need to analyze the existence of purely imaginary roots of the characteristic equation. Suppose $i\omega$ $(\omega > 0)$ is a root of (3.8), then by substituting $\lambda = i\omega$ into (3.8), we obtain

$$\begin{cases} -\omega^2 + B_n = -C_n w\sin(\omega\tau) - D_n\cos(\omega\tau), \\ A_n\omega = -C_n\omega\cos(\omega\tau) + D_n\sin(\omega\tau), \end{cases} \tag{3.10}$$

thus ω satisfies

$$\omega^4 + (A_n^2 - 2B_n - C_n^2)\omega^2 + (B_n^2 - D_n^2) = 0. \tag{3.11}$$

Solving (3.11) for ω^2, we get

$$\left(\omega_n^\pm\right)^2 = \frac{1}{2}\left[-(A_n^2 - 2B_n - C_n^2) \pm \sqrt{(A_n^2 - 2B_n - C_n^2)^2 - 4(B_n^2 - D_n^2)}\right], \tag{3.12}$$

where

$$\begin{aligned}A_n^2-2B_n-C_n^2&=(d_1^2+d_2^2)\frac{n^4}{l^4}+2d_2(pu_*+q)\frac{n^2}{l^2}+(pu_*+q)^2+2mpu_*w_*-\frac{r^2}{K^2}{u_*}^2,\\ B_n^2-D_n^2&=(B_n+D_n)(B_n-D_n)\\ &=(B_n+D_n)\left[d_1d_2\frac{n^4}{l^4}+(d_1pu_*+d_1q-\frac{d_2r}{K}u_*)\frac{n^2}{l^2}-\frac{r}{K}(pu_*+q)u_*-mpu_*w_*\right].\end{aligned}$$

Since $B_n+D_n>0$, $B_n^2-D_n^2$ has the same sign as B_n-D_n. Note that B_n-D_n is a quadratic function with respect to n^2 whose graph opens upward and $B_0-D_0=-r(pu_*+q)u_*/K-mpu_*w_*<0$. Hence there exists a positive number

$$N_0=\sqrt{l^2\frac{-\left(d_1pu_*+d_1q-\frac{d_2r}{K}u_*\right)+\sqrt{\triangle_1}}{2d_1d_2}},$$

where $\triangle_1=\left(d_1pu_*+d_1q-\frac{d_2r}{K}u_*\right)^2+4d_1d_2\left[\frac{r}{K}(pu_*+q)u_*+mpu_*w_*\right]$, such that

$$B_n^2-D_n^2\begin{cases}<0, \text{ if } 0\le n<N_0,\\ >0, \text{ if } n>N_0.\end{cases}$$

If $\pm i\omega_n^{\pm}$ are two pairs of imaginary roots of the the characteristic equation (3.8), then from (3.10), we find that the corresponding delay values are

$$\tau_{n,j}^{\pm}=\begin{cases}\frac{1}{\omega_n^{\pm}}\arccos\left\{\frac{(D_n-A_nC_n)(\omega_n^{\pm})^2-B_nD_n}{C_n^2(\omega_n^{\pm})^2+D_n^2}\right\}+\frac{2j\pi}{\omega_n^{\pm}}, & \sin\left(\omega_n^{\pm}\tau_{n,j}^{\pm}\right)>0,\\ \frac{1}{\omega_n^{\pm}}\left[2\pi-\arccos\left\{\frac{(D_n-A_nC_n)(\omega_n^{\pm})^2-B_nD_n}{C_n^2(\omega_n^{\pm})^2+D_n^2}\right\}\right]+\frac{2j\pi}{\omega_n^{\pm}}, & \sin\left(\omega_n^{\pm}\tau_{n,j}^{\pm}\right)<0.\end{cases}\tag{3.13}$$

Moreover, from (3.10) we can deduce that

$$\sin\left(\omega_n^{\pm}\tau_{n,j}^{\pm}\right)=\frac{C_n(\omega_n^{\pm})^3+(A_nD_n-B_nC_n)\,\omega_n^{\pm}}{C_n^2(\omega_n^{\pm})^2+D_n^2}.$$

In terms of the expressions of A_n, D_n, B_n, C_n, we can get $A_nD_n-B_nC_n>0$, therefore the expression of $\tau_{n,j}^{\pm}$ is actually given by the first equation of (3.13), that is,

$$\tau_{n,j}^{\pm}=\frac{1}{\omega_n^{\pm}}\arccos\left\{\frac{(D_n-A_nC_n)(\omega_n^{\pm})^2-B_nD_n}{C_n^2(\omega_n^{\pm})^2+D_n^2}\right\}+\frac{2j\pi}{\omega_n^{\pm}}.$$

Assume $\lambda(\tau)=\alpha(\tau)+\beta(\tau)$ is the root of the characteristic equation (3.8) satisfying $\alpha(\tau_{n,j}^{\pm})=0, \beta(\tau_{n,j}^{\pm})=i\omega_n^{\pm}$, then using the similar arguments as in Lemma 2.2, we can get the following transversality conditions.

Lemma 3.3. *The following statements hold.*

(i) *If $0\le n<N_0$, then the characteristic equation (3.8) has a purely imaginary root $i\omega_n^+$,and it satisfies $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\lambda(\tau_{n,j}^+)>0$.*

(ii) *If $n>N_0$ and $A_n^2-2B_n-C_n^2<0$ hold for some n,*
   - (a) *if $(A_n^2-2B_n-C_n^2)^2-4(B_n^2-D_n^2)>0$, then the characteristic equation (3.8) has two purely imaginary roots $i\omega_n^+$ and $i\omega_n^-$, they satisfy $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\lambda(\tau_{n,j}^+)>0, \frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\lambda(\tau_{n,j}^-)<0$;*
   - (b) *if $(A_n^2-2B_n-C_n^2)^2-4(B_n^2-D_n^2)=0$, then the characteristic equation (3.8) has a purely imaginary root $i\omega^+=i\omega^-$, it satisfies $\frac{\mathrm{d}}{\mathrm{d}\tau}\mathrm{Re}\lambda(\tau_{n,j}^{\pm})=0$;*
   - (c) *if $(A_n^2-2B_n-C_n^2)^2-4(B_n^2-D_n^2)<0$, then the characteristic equation (3.8) has no purely imaginary root.*

(iii) *If $n>N_0$ and $A_n^2-2B_n-C_n^2\ge 0$ hold for some n, then the characteristic equation (3.8) has no purely imaginary root.*

Let

$$\mathcal{D}_1 = \left\{ n \in \mathbb{N}_0 : n > N_0, A_n^2 - 2B_n - C_n^2 < 0, (A_n^2 - 2B_n - C_n^2)^2 - 4(B_n^2 - D_n^2) > 0 \right\}.$$

It is clear that $\{\tau_{n,j}^{\pm}\}|_{j=0}^{\infty}$ is monotonically increasing with respect to j for the fixed $n \in \mathcal{D}_1$, therefore $\tau_{n,0}^{\pm} = \min\left\{\tau_{n,j}^{\pm}\right\}$ for fixed n. According to Theorem 3.2, if $h < h_2$ and $\tau = 0$, the coexistence equilibrium (u_*, w_*) is stable, then $\tau_{n,0}^{+} < \tau_{n,0}^{-}$. We define the critical delay value τ^* where the first stability change of (u_*, w_*) will happen, which can be

$$\tau^* =: \tau_{n_0,0}^{+} = \min\left\{\tau_{n,0}^{+}\right\}, \text{ if } n \in \mathcal{D}_1 \cup \{n \in \mathbb{N}_0 : 0 \le n \le N_0\}.$$

Based on Theorem 3.2, Lemma 3.3, we can deduce the following theorem.

Theorem 3.4. *Assume that condition $h < h_2$ hold. Then*

(i) *when $0 \le \tau < \tau^*$, (u_*, w_*) is locally asymptotically stable.*
(ii) *when $\tau = \tau^*$, the Hopf bifurcation is generated at (u_*, w_*).*
(iii) *when $\tau > \tau^*$, (u_*, w_*) is unstable.*

Proof. From the above analysis, τ^* is the critical delay value that the first stability change of (u_*, w_*) will happen. Therefore combining Theorem 3.2 and Lemma 3.3, we can deduce that when $0 \le \tau < \tau^*$, all roots of (3.8) have negative real parts. When $\tau = \tau^*$, the n_0th characteristic equation has a pair of purely imaginary roots, and the roots of the remaining characteristic equation still have negative real parts. If $\tau > \tau^*$, the characteristic equation (3.8) has at least one pair of roots with positive real part. The theorem is proved. □

Theorem 3.5. *If $h_1 < h < h_2$, then the coexistence steady state (u^*, w^*) is unstable with the RDE system (1.2).*

Proof. According to Theorem 2.4, (u^*, w^*) is unstable in system (1.1), which indicates the characteristic equation of system (1.2) at (u^*, w^*) has at least one root with real part greater than zero when n=0, therefore (u^*, w^*) is unstable. □

4. Numerical results

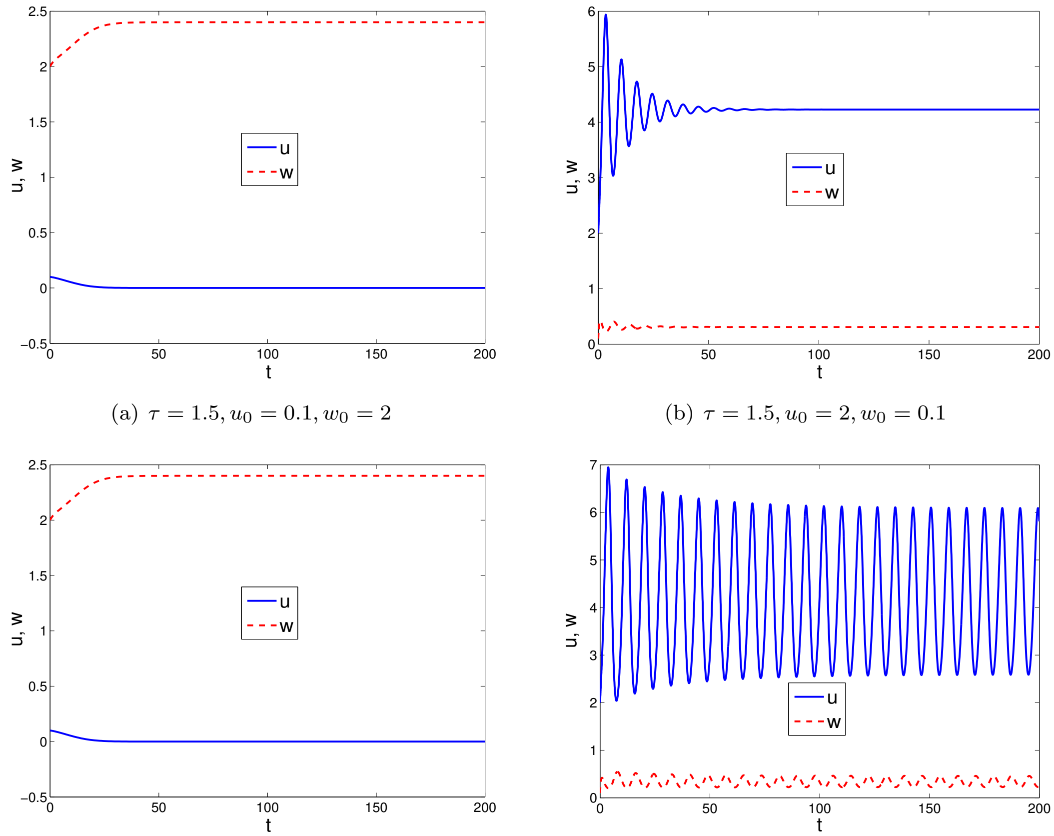
In this section, we verify the theoretical results obtained in sections 2 and 3 by numerically solving the DDE system (1.1) and the RDE system (1.2). In particular, we choose the following model parameters:

$$r = 1, k = 5, m = 0.5, h = 1.2, p = 0.8, q = 0.5, \tag{4.1}$$

such that the condition $h_1 < h < h_2$ is satisfied. With these parameters, when $\tau = 0$, both the toxicant-only equilibrium $(0, \bar{w}) \approx (0, 2.400)$ and the coexistence equilibrium $(u_*, w_*) \approx (4.227, 0.309)$ are locally asymptotically stable (see Table 1), that is, system (1.1) exhibits bistability. In addition, using the set of parameters (4.1) and equation (2.8), we are able to obtain $\tau_0^+ = 1.753$.

Figure 1 shows the effects of the initial condition and the delay τ on the stability of the equilibria $(0, \bar{w})$ and (u_*, w_*) in the DDE system (1.1). As we can see from Figure 1, when the initial condition is close to $(0, \bar{w})$, the solution of system (1.1) will converges to $(0, \bar{w})$, regardless of the value of τ (Figure 1(a) and Figure 1(c)). On the other hand, if the initial condition is close to (u_*, w_*), the solution will converges to (u_*, w_*) when $\tau < \tau_0^+$ (Figure 1(b)), and system (1.1) has a periotic solution when $\tau > \tau_0^+$ (Figure 1(d)).

Figure 2 demonstrates the stability of spatially homogeneous steady states of the reaction-diffusion system (1.2). Again, we observe that when $\tau < \tau_0^+$, system (1.2) exhibits bistability, that is, depending on the initial distributions, either $(0, \bar{w})$ is linearly stable or (u_*, w_*) is linearly stable. When $\tau > \tau_0^+$, either $(0, \bar{w})$ is linearly stable or system (1.2) has a time-periodic solution.



(a) $\tau = 1.5, u_0 = 0.1, w_0 = 2$

(b) $\tau = 1.5, u_0 = 2, w_0 = 0.1$

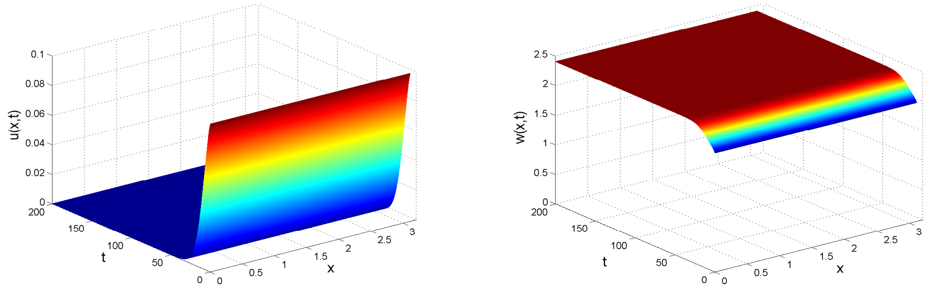
(c) $\tau = 1.8, u_0 = 0.1, w_0 = 2$

(d) $\tau = 1.8, u_0 = 2, w_0 = 0.1$

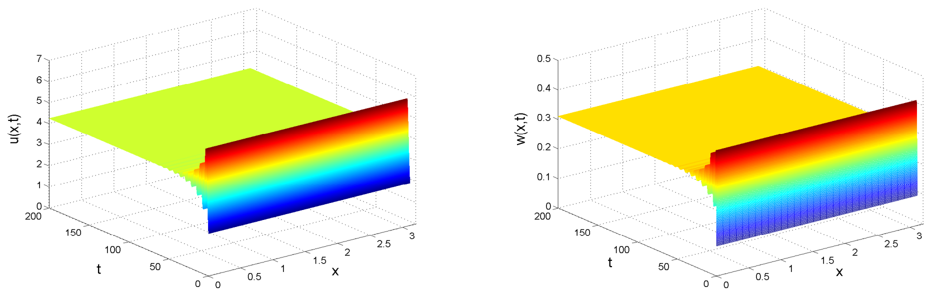
FIGURE 1. Numerical solutions of the DDE model (1.1) with different initial conditions and time delays.

5. Discussion

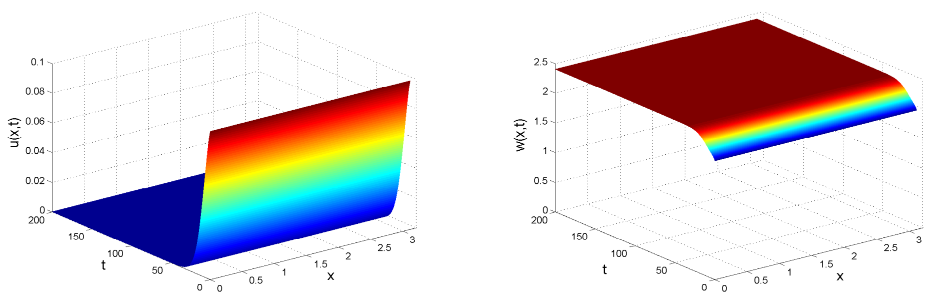
The effects of environmental toxicants on aquatic life is of great importance from both environmental and conservation points of view. Over the past few decades, the development of ecotoxicological models has played a crucial role in enhancing our comprehension and assessment of how toxicants impact population dynamics. Traditional population-toxicant interaction models assume the population growth is instantaneous, even though there may be potential time delays attributable to reproductive and maturation processes. In this paper, we introduced and investigated two models with time delays to explore the interaction between a population and a toxicant, where the population growth is governed by a delayed logistic equation or Hutchinson equation. We mainly focused on the local stability analysis of the steady states of the models. Our findings indicate that high toxicant concentrations ($h > h_2$) result in population extinction, whereas moderate toxicant levels ($h_1 < h < h_2$) can potentially induce bistability. In the case of bistability, the population's fate, whether persistence or extinction, depends on the initial densities of the population and toxicant. Furthermore, both our theoretical analysis and numerical simulations demonstrate that the introduction of a time delay can lead to the destabilization of the coexistence equilibrium (u_*, w_*) and the appearance of periodic solutions through Hopf bifurcation.



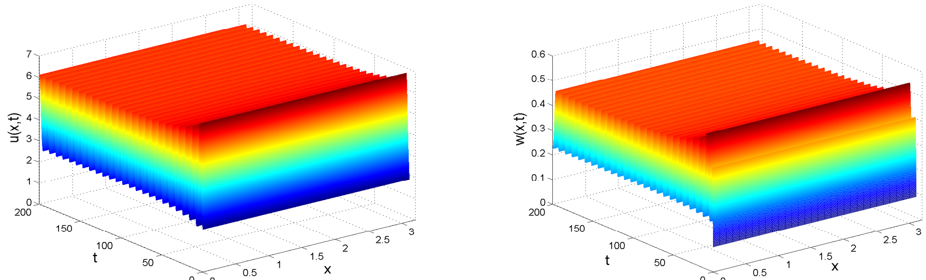
(a) $\tau = 1.5, u_0 = 0.1, w_0 = 2$



(b) $\tau = 1.5, u_0 = 2, w_0 = 0.1$



(c) $\tau = 1.8, u_0 = 0.1, w_0 = 2$



(d) $\tau = 1.8, u_0 = 2, w_0 = 0.1$

FIGURE 2. Numerical solutions of the RDE model (1.2) with different initial conditions and time delays. Parameters: $d_1 = 1, d_2 = 1$, the other parameters are the same as in Figure 1.

However, the time delay does not affect the stability of the toxicant-only equilibrium $(0, \bar{w})$ and the coexistence equilibrium (u^*, w^*).

There are at least two issues we are unable to solve: (i) We focused solely on examining the local stability of the steady states in systems (1.1) and (1.2). We believe that conducting a comprehensive analysis involving global stability and bifurcation will offer deeper insights into the influence of the toxicant on the long-term dynamics of the population. (ii) Our numerical findings indicate a concurrence between the two critical values, namely, τ_0^+ in Theorem 2.3 and τ^* in Theorem 3.4, where Hopf bifurcations occur. It is important to establish this consistency through a rigorous theoretical proof. We leave the aforementioned two issues for future research endeavors.

The current models have the potential for generalization in several biologically meaningful manners: (i) In models (1.1) and (1.2), the toxicant input rate is assumed to remain constant. Nonetheless, in real-world scenarios, toxicants are often discharged into water bodies at specific times and locations. Incorporating temporally and spatially varying input rates of the toxicant would yield a more accurate and realistic model. (ii) Numerous species inhabit environments characterized by unidirectional flows, such as rivers and streams. Introducing an advection term into model (1.2) to account for the effects of this unidirectional flow will result in a reaction-diffusion-advection model. (iii) Model (1.1) assumes that the impact of toxicity on population growth is instantaneous. Nevertheless, in cases where a species resides in a contaminated aquatic environment, toxicants may exert delayed effects on its reproductive and mortality rates [2, 23]. By incorporating delayed toxic responses, one can extend model (1.1) to the following model with two discrete delays:

$$\begin{cases} \frac{\mathrm{d}u(t)}{\mathrm{d}t} = ru(t)(1 - \frac{u(t-\tau_1)}{K}) - mw(t-\tau_2)u(t), \\ \frac{\mathrm{d}w(t)}{\mathrm{d}t} = h - pu(t)w(t) - qw(t), \end{cases} \tag{5.1}$$

where the time delay τ_2 represents the delayed toxic response. Moreover, taking spatial dispersal into account, one can further extend model (5.1) to a reaction-diffusion model with two discrete delays.

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