DYNAMICS OF A DIFFUSIVE NUTRIENT-PHYTOPLANKTON-ZOOPLANKTON MODEL WITH SPATIO-TEMPORAL DELAY*

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Abstract. We study a diffusive nutrient-phytoplankton-zooplankton (NPZ) model with spatio-temporal delay. The closed nature of the system allows the formulation of a conservation law of biomass that governs the ecosystem. We advance the understanding of the local stability for equilibrium solutions of the NPZ model by proposing a new local stability theorem for generalized three-dimensional systems. Using a specific delay kernel, we perform a qualitative analysis of the solutions, including existence, uniqueness, and boundedness of the solutions, global stability of the trivial equilibrium, and Hopf bifurcation of the nontrivial equilibrium. Numerical simulations are also performed to verify and supplement our analytical results. We show that diffusion predominantly has a stabilizing effect; however, if sufficient nutrient is present, complex spatio-temporal dynamics may occur.

1. Introduction. Plankton are drifting organisms that live in the oceans, lakes, and rivers, and play a fundamental role in the global carbon cycle and marine food webs. Three important trophic compartments in virtually all acquatic ecosystems are nutrients, phytoplankton, and zooplankton. In a closed ecosystem, the total biomass is conserved. This is why it is of interest to investigate nutrient-phytoplankton-zooplankton (NPZ) models that are conservative, that is, where no mass is added to or subtracted from the system [7, 17, 18, 19]. Sources and sinks can be easily added afterwards, but it is of interest to first better understand how the closed system behaves.

It is known that nutrient recycling takes time, which has been studied in several papers [1, 13, 14, 17, 18, 24]. Beretta, Bischi, and Solimano used a distributed delay term to describe the dynamics of the nutrient recycling [1]. This type of delay has been studied frequently in chemostat-type models [13, 14, 24]. In [17], Kloosterman, Campbell, and Poulin considered a closed NPZ model with a delay in the nutrient recycling to investigate how a planktonic ecosystem is affected by the quantity of biomass it contains and by the properties of the delay distribution. Further, the authors incorporated a size structure in the juvenile zooplankton with the NPZ model and showed the key roles of the total biomass in the system and the maturity level of zooplankton [18]. The pioneering works above [1, 13, 14, 17, 18, 24] mainly focused on spatially homogeneous models with time delay. This is beneficial in that

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one can obtain analytical results relatively easily, but this approach completely neglects spatial effects. Since nutrients, phytoplankton, and zooplankton are generally inhomogeneously distributed in space it is important to better understand the effect of spatial effects, such as advection, diffusion, and turbulence. Therefore, it is more complicated, but also more realistic, to consider an NPZ model with diffusion and time delay. Moreover, to account for the drift of individuals to their present position from all possible positions at previous times, a weighted spatial-average delay term was first introduced in [10] and then developed in [3, 12, 25, 26, 28].

The plan for this paper is as follows. In section 2 we present the model with diffusion and spatio-temporal delay, obtain the conservation law for the closed ecosystem, and describe the spatially uniform equilibria. In section 3 we formulate conditions for the local stability of a uniform equilibrium for a generalized three-dimensional diffusion-reaction model and then give the local stability analysis for the equilibria of the NPZ model. In section 4 we discuss existence, uniqueness, the global stability of solutions, and the Hopf bifurcation of the NPZ model with a weak delay kernel. In section 5 we use numerical simulations to verify and supplement our analytical results and to investigate the influence of certain perturbations. In section 6 we summarize and conclude our findings and discuss their implications.

2. Modeling and equilibrium solutions. The model consists of an NPZ model based on that of [17] that includes a spatio-temporal delay and Laplacian diffusion. In this model the components are nutrient $N(x,t)$, phytoplankton $P(x,t)$, and zooplankon $Z(x,t)$ at location x and time t. For simplicity, we only consider the one space dimension. We take $x \in [0, l\pi]$ as the depth within the water column, where 0 is the top of the column and $l\pi$ is the bottom. A simplified schematic of the model is shown in Figure 1, which shows the flow of biomass between the components.

Diffusion in NPZ models can arise from various mechanisms. One is due to the physics and arises of the motion of the water around the organisms. Another is due to the biology, as species tend to spread out to lower their gradients of concentration. The former would yield diffusion rates that are similar for each species, whereas the latter would yield rather different diffusion rates. In this work we choose the diffusion rates to be equal to model the effects of the physics only. Also, this is the simplest choice as it reduces the number of parameters that must be set.

Our model then takes the form

$$(2.1) \quad \begin{cases} N_t(x,t) = dN_{xx} - \mu P(x,t)f(N(x,t)) + \delta(M_2 * Z)(x,t) + \lambda(M_1 * P)(x,t) \\ \qquad\qquad + (1-r)g(M_3 * Zh(P))(x,t), \\ P_t(x,t) = dP_{xx} + \mu P(x,t)f(N(x,t)) - gZ(x,t)h(P(x,t)) - \lambda P(x,t), \\ Z_t(x,t) = dZ_{xx} + rgZ(x,t)h(P(x,t)) - \delta Z(x,t) \end{cases}$$
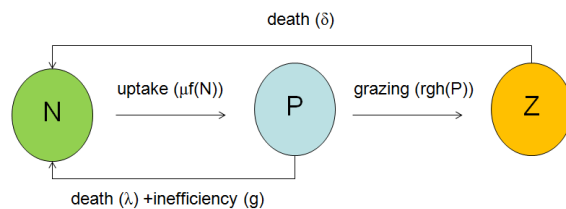

FIG. 1. *Simplified schematic of model.*

for $t > 0$ and $x \in (0, l\pi)$. The spatio-temporal delay terms are defined by

$$(2.2) \qquad (M_i * u)(x,t) = \int_{-\infty}^{t} \int_{0}^{l\pi} M_i(x,y,t-s)u(y,s)\mathrm{d}y\mathrm{d}s$$

$$= \int_{-\infty}^{t} \int_{0}^{l\pi} G(x,y,t-s)m_i(t-s)u(y,s)\mathrm{d}y\mathrm{d}s.$$

This type of delay term calculates the probability of an individual having been at point y at the earlier time s, given that it is at point x at the current time t. The function $m_i : [0, \infty) \to \mathbb{R}^+$ is the delay kernel, which weights the population t time units in the past and satisfies $m_i(t) \geq 0$ for all $t \geq 0$. The function $G : (0, l\pi) \times (0, l\pi) \times (0, \infty) \to \mathbb{R}^+$ is a probability density function, which is chosen from the appropriately normalized solution of the heat equation,

$$(2.3) \qquad \begin{cases} G_t = dG_{yy}, & y \in (0, l\pi), \\ G_y = 0, & y = 0, \ l\pi, \\ G(x,y,0) = \delta(x-y), & x, y \in [0, l\pi]. \end{cases}$$

These functions satisfy the normalization conditions

$$(2.4) \qquad \int_{0}^{\infty} m_i(t)\mathrm{d}t = 1 \ \text{ and } \ \int_{0}^{l\pi} G(x,y,t)\mathrm{d}x = 1, \ \ y \in (0, l\pi), \ \ t \geq 0.$$

Since the domain is closed, we impose no flux (Neumann) boundary conditions,

$$(2.5) \qquad \frac{\partial N}{\partial x} = \frac{\partial P}{\partial x} = \frac{\partial Z}{\partial x} = 0, \quad t > 0, \quad x = 0, l\pi.$$

For biological plausibility, the system should be positive, which is to say that all the state variables take nonnegative values for $t \geq 0, x \in (0, l\pi)$. Thus the initial conditions are chosen so that each component is nonnegative:

$$(2.6) \qquad N(x,t) = N_0(x,t) \geq 0, \quad P(x,t) = P_0(x,t) \geq 0,$$

$$Z(x,t) = Z_0(x,t) \geq 0, \quad t \in (-\infty, 0], \quad x \in (0, l\pi).$$

The model parameters are defined in Table 1. All parameters in the model are assumed to be positive, and we further restrict $r \in (0, 1]$. For the computations the parameters will take the values given in Table 1.

TABLE 1

Parameter meanings and values used for all computations. The biological parameters values are from [22].

Parameter	Meaning	Value
d	diffusion constant	varies
l	domain size factor	2
μ	phytoplankton maximum birth rate	5.9 day^{-1}
λ	phytoplankton death rate	0.017 day^{-1}
g	zooplankton maximum grazing rate	7 day^{-1}
r	zooplankton assimilation efficiency	0.7
δ	zooplankton death rate	0.17 day^{-1}
τ	the mean delay	7 day
Function	Meaning	Value
$f(N)$	phytoplankton nutrient uptake function	$\frac{N}{N+1}$
$h(P)$	zooplankton grazing function	$\frac{P}{P+1}$

The functions $f(N)$ and $h(P)$ are related to the uptake of nutrient by phytoplankton and the grazing of zooplankton on phytoplankton, respectively. Since these functions are related to the growth of the phytoplankton and zooplankton, the functions should be zero at zero and positive otherwise. Further, modeling studies have indicated that these should be increasing functions, indicating that there is more growth when more nutrient is present, and bounded above, representing satiation of the organisms [8, 17, 22]. Finally, the phytoplankton uptake function is typically taken to be concave down [8, 17, 22]. Thus we assume $f, g \in \mathbb{C}^2$ and have the following properties:

$$f(0) = 0, \quad f'(N) > 0, \quad f''(N) < 0, \quad \lim_{N \to \infty} f(N) = 1,$$
$$h(0) = 0, \quad h'(P) > 0, \quad \lim_{P \to \infty} h(P) = 1.$$

To our knowledge, the proof of existence, uniqueness, and positivity of solutions of the model (2.1)–(5.1) with general delay kernels, $m_i(t)$, is an open problem. In section 4 we will prove this for the specific case where $m_i(t)$ are gamma distributions. Our results in section 3.2 will apply to any delay kernel for which existence, uniqueness, and positivity hold.

Since (2.1) is closed, there is no biomass lost or gained in the ecosystem. Consequently, there is a conservation law, which is obtained by adding the equations in (2.1), integrating x on the interval $(0, l\pi)$, and applying the boundary conditions (2.5) to yield

$$
\begin{aligned}
(2.7) \quad & \int_0^{l\pi} (P_t(x,t) + N_t(x,t) + Z_t(x,t)) \mathrm{d}x \\
& = \frac{\mathrm{d}}{\mathrm{d}t} \left[\lambda \int_0^{l\pi} \int_0^\infty \int_t^{t-\eta} M_1(x,y,\eta) P(x,\nu) \mathrm{d}\nu \mathrm{d}\eta \mathrm{d}x \right. \\
& \quad + \delta \int_0^{l\pi} \int_0^\infty \int_t^{t-\eta} M_2(x,y,\eta) Z(x,\nu) \mathrm{d}\nu \mathrm{d}\eta \mathrm{d}x \\
& \quad \left. + (1-r)g \int_0^{l\pi} \int_0^\infty \int_t^{t-\eta} M_3(x,y,\eta) Z(x,\nu) h(P(x,\nu)) \mathrm{d}\nu \mathrm{d}\eta \mathrm{d}x \right].
\end{aligned}
$$

Thus we obtain the following expression for the total biomass in the system:

$$
\begin{aligned}
(2.8) \\
\tilde{N}_T = & \int_0^{l\pi} (P(x,t) + N(x,t) + Z(x,t)) \mathrm{d}x + \lambda \int_0^{l\pi} \int_0^\infty \int_{t-\eta}^t M_1(x,y,\eta) P(y,\nu) \mathrm{d}\nu \mathrm{d}\eta \mathrm{d}x \\
& + \delta \int_0^{l\pi} \int_0^\infty \int_{t-\eta}^t M_2(x,y,\eta) Z(x,\nu) \mathrm{d}\nu \mathrm{d}\eta \mathrm{d}x \\
& + (1-r)g \int_0^{l\pi} \int_0^\infty \int_{t-\eta}^t M_3(x,y,\eta) Z(x,\nu) h(P(x,\nu)) \mathrm{d}\nu \mathrm{d}\eta \mathrm{d}x,
\end{aligned}
$$

which remains constant in time. In particular, $\tilde{N}_T$ will be determined by the initial data (2.6); thus we assume that initial data is such that the integrals in (2.8) are finite. Further, if the model admits a spatially uniform equilibrium solution (N^*, P^*, Z^*), the conservation law (2.8) simplifies to the following:

$$(2.9) \qquad N_T = \lambda P^* T_1 + \delta Z^* T_2 + (1-r)g Z^* h(P^*) T_3 + P^* + N^* + Z^*,$$

where T_i is the mean delay, defined by $T_i = \int_0^\infty \eta m_i(\eta) d\eta, i = 1, 2, 3$.

We begin by studying the equilibrium solutions of model (2.1). The equations (2.4) imply that the nonlocal delay terms have no effect on the spatially uniform steady state solutions. Since the state variables represent concentrations, only non-negative solutions are meaningful; therefore, we will say an equilibrium solution does not exist if any of the components are negative.

There are three types of spatially uniform equilibrium solutions. The first is the trivial equilibrium. We set $P = Z = 0$; then from the conservation law, we find $N = N_T$. This equilibrium solution will be referred to as $E_1 = (N_1, P_1, Z_1) = (N_T, 0, 0)$. This solution exists if $N_T \geq 0$. Biologically this represents the states where there is no life in the ecosystem and all the biomass is in the nutrient. The second type of equilibrium is in the form $E_2 = (N_2, P_2, 0)$ with $N_2 > 0$ and $P_2 > 0$. A necessary condition for this equilibrium to exist is

$$(2.10) \qquad \mu > \lambda,$$

since f is an increasing function with $0 \leq f(N) < 1$. Biologically this means the maximum growth rate of phytoplankton must be greater than its death rate. If this is true, $N_2 = f^{-1}(\frac{\lambda}{\mu})$, and, from the conservation law, $P_2 = \frac{N_T - N_2}{1 + \lambda T_1}$. It is clear that this equilibrium point exists if and only if

$$(2.11) \qquad N_T > f^{-1}\left(\frac{\lambda}{\mu}\right).$$

The third type of equilibrium is in the form (N_3, P_3, Z_3) with $N_3 > 0$, $P_3 > 0$, $Z_3 > 0$. A necessary condition for this equilibrium solution to exist is

$$(2.12) \qquad rg > \delta,$$

which means that the product of the maximum growth rate of the zooplankton and the assimilation efficiency must be greater than its death rate. If (2.12) is satisfied, then $P_3 = h^{-1}(\frac{\delta}{rg})$, $Z_3 = \frac{(\mu f(N_3) - \lambda)P_3 r}{\delta}$. From the conservation law, N_3 satisfies the following implicit expression:

$$(2.13) \qquad N_3 = N_T - (\lambda T_1 + 1)P_3 + (\delta T_2 + 1)Z_3 + (1 - r)Z_3 \frac{\delta}{r} T_3.$$

Note that this equilibrium point only exists if $Z_3 > 0$, that is,

$$(2.14) \qquad \mu f(N_3) - \lambda > 0.$$

In summary, the spatially homogeneous equilibria are given by

$$E_1 = (N_T, 0, 0), \ E_2 = \left(f^{-1}\left(\frac{\lambda}{\mu}\right), \frac{N_T - f^{-1}(\frac{\lambda}{\mu})}{1 + \lambda T_1}, 0\right),$$

$$E_3 = \left(N_3, h^{-1}\left(\frac{\delta}{rg}\right), \frac{(\mu f(N_3) - \lambda)P_3 r}{\delta}\right),$$

where N_3 satisfies (2.13). Note that, due to the monotonicity of f and h, there is a unique equilibrium of each type for any value of N_T such that the equilibrium exists.

3. Local stability of uniform equilibria. This section first derives a local stability result for a general reaction-diffusion problem with a spatio-temporal delay and then specializes the result to the particular NPZ model of interest.

3.1. Local stability of the general reaction-diffusion model. In this subsection, we study the local asymptotic stability of the following general reaction-diffusion model with spatio-temporal delays in a bounded domain under Neumann boundary condition:

(3.1)
$$
\begin{cases}
\dfrac{\partial u_1}{\partial t} = d\dfrac{\partial^2 u_1}{\partial x^2} + F_1(x,t,u_1,u_2,u_3,q,M*\bar{\mathbf{f}}(u_2,u_3)), & t>0, \quad x \in (0,l\pi), \\[2mm]
\dfrac{\partial u_2}{\partial t} = d\dfrac{\partial^2 u_2}{\partial x^2} + F_2(x,t,u_1,u_2,u_3,q), & t>0, \quad x \in (0,l\pi), \\[2mm]
\dfrac{\partial u_3}{\partial t} = d\dfrac{\partial^2 u_3}{\partial x^2} + F_3(x,t,u_1,u_2,u_3,q), & t>0, \quad x \in (0,l\pi), \\[2mm]
\dfrac{\partial u_1}{\partial x} = \dfrac{\partial u_2}{\partial x} = \dfrac{\partial u_3}{\partial x} = 0, & t>0, \quad x = 0, l\pi, \\[2mm]
u_1(x,t)=u_1(x)\geq 0, u_2(x,t)=u_2(x)\geq 0, \quad u_3(x,t)=u_3(x)\geq 0, & t \in (-\infty,0], \ x \in [0,l\pi],
\end{cases}
$$

where q is simply a list of all the parameters. $F_i : U \to \mathbb{R}$ is continuously differentiable, where U is an open interval, and there exists $\theta \in U$ such that $F(\theta) = 0$. $F_{1,2,3}$ are, in general, nonlinear functions of $u_{1,2,3}$ and $M*\bar{\mathbf{f}}(u_2,u_3)$. Here, $M*\bar{\mathbf{f}}(u_2,u_3) = (M_1*\bar{f}_1(u_2,u_3),\ldots,M_k*\bar{f}_k(u_2,u_3))$ represents the spatio-temporal delays, as defined in (2.2). The components of $\bar{\mathbf{f}} : \mathbb{R}^2 \to \mathbb{R}^k$ may be a linear or nonlinear functions of u_2, u_3.

Assume that system (3.1) has a spatially homogeneous, nonnegative equilibrium (u_1^*, u_2^*, u_3^*), which satisfies

$$
F_1(u_1^*,u_2^*,u_3^*,q,M*\bar{\mathbf{f}}(u_2^*,u_3^*)) = 0, \ F_2(u_1^*,u_2^*,u_3^*,q) = 0, \ F_3(u_1^*,u_2^*,u_3^*,q) = 0.
$$

The linearization about this equilibrium solution is

(3.2)
$$
\begin{cases}
\dfrac{\partial u_1}{\partial t} = d\dfrac{\partial^2 u_1}{\partial x^2} + A_{11}(q)u_1 + A_{12}(q,\mathbf{M})*u_2 + A_{13}(q,\mathbf{M})*u_3, \\[2mm]
\dfrac{\partial u_2}{\partial t} = d\dfrac{\partial^2 u_2}{\partial x^2} + A_{21}(q)u_1 + A_{22}(q)u_2 + A_{23}(q)u_3, \\[2mm]
\dfrac{\partial u_3}{\partial t} = d\dfrac{\partial^2 u_3}{\partial x^2} + A_{31}(q)u_1 + A_{32}(q)u_2 + A_{33}(q)u_3,
\end{cases}
$$

where $\mathbf{M} = (M_1,\ldots,M_k)$, and $A_{12(3)}$ are linear functions of the M_i.

Solving the model (2.3) in a similar manner to [9] we find

$$
G(x,y,t) = \frac{1}{l\pi} + \frac{2}{l\pi}\sum_{n=1}^{\infty} e^{-d\frac{n^2}{l^2}t}\cos\frac{n}{l}x\cos\frac{n}{l}y.
$$

Under the homogeneous Neumann boundary conditions, the appropriate trial solution is

(3.3) $$(u_1,u_2,u_3) = (c_1,c_2,c_3)e^{\phi t}\cos\frac{n}{l}x, \ n = 0,1,2,\ldots$$

Using this trial solution, the term (2.2) can be written as

$$
(M_i*u)(x,t) = \int_{-\infty}^{t}\int_0^{l\pi} G(x,y,t-s)m_i(t-s)e^{\phi s}\cos\frac{n}{l}y\,dy\,ds.
$$

After some algebra [11], we find that

$$(M_i * u)(x,t) = \mathscr{M}_i\left(\phi + \frac{dn^2}{l^2}\right)e^{\phi t}\cos nx.$$

Here, $\mathscr{M}_i$ denotes the Laplace transform of m_i. For later use, we note that, for any kernel m_i,

$$(3.4) \qquad \mathscr{M}_i\left(iR + \frac{dn^2}{l^2}\right) = \int_0^\infty m_i(t)e^{-\left(iR + \frac{dn^2}{l^2}\right)t}\mathrm{d}t = \mathscr{C}_i(R,n) - i\mathscr{S}_i(R,n),$$

where $\mathscr{C}_i(R,n) = \int_0^\infty m_i(t)e^{-\frac{dn^2}{l^2}t}\cos Rt\mathrm{d}t$, $\mathscr{S}_i(R,n) = \int_0^\infty m_i(t)e^{-\frac{dn^2}{l^2}t}\sin Rt\mathrm{d}t$. For $i \in \mathbb{N}$ and $n \geq 0$, it follows from (2.4) that

$$|\mathscr{C}_i(R,n)| \leq 1 \qquad \text{and} \qquad |\mathscr{S}_i(R,n)| \leq 1$$

with $\mathscr{C}_i(0,0) = 1$ and $\mathscr{S}_i(0,0) = 0$. Further,

$$
\begin{aligned}
(3.5) \qquad |\mathscr{S}_i(R,n)| &\leq \int_0^\infty m_i(t)e^{-\frac{dn^2}{l^2}t}|\sin Rt|\mathrm{d}t \leq \int_0^\infty m_i(t)e^{-\frac{dn^2}{l^2}t}Rt\mathrm{d}t \\
&\leq R\int_0^\infty m_i(t)t\mathrm{d}t = RT_i
\end{aligned}
$$

and

$$(3.6) \qquad \left.\frac{\mathrm{d}\mathscr{S}_i(R,n)}{\mathrm{d}R}\right|_{R=0} = \int_0^\infty m_i(t)te^{-\frac{dn^2}{l^2}t}\mathrm{d}t \leq T_i.$$

Substituting (3.3) into (3.2), we obtain the characteristic equation

$$(3.7) \qquad \Phi(\phi,n^2,q) = -\phi^3 + B_2(n^2,q)\phi^2 + B_1(\phi,n^2,q)\phi + B_0(\phi,n^2,q) = 0$$

with

$$
\begin{aligned}
B_2(n^2,q) &= A_{11} + A_{22} + A_{33} - 3\frac{dn^2}{l^2}, \\
B_1(\phi,n^2,q) &= A_{12}(\mathscr{M})A_{21} + A_{13}(\mathscr{M})A_{31} + A_{23}A_{32} + 2\frac{dn^2}{l^2}(A_{11} + A_{22} + A_{33}) \\
&\quad - A_{22}A_{33} - A_{11}(A_{22} + A_{33}) - 3\frac{d^2n^4}{l^4}, \\
B_0(\phi,n^2,q) &= A_{12}(\mathscr{M})\left(A_{23}A_{31} - A_{21}A_{33} + A_{21}\frac{dn^2}{l^2}\right) \\
&\quad + A_{13}(\mathscr{M})\left(A_{21}A_{32} + A_{31}\frac{dn^2}{l^2} - A_{22}A_{31}\right) \\
&\quad + \left(A_{11} - \frac{dn^2}{l^2}\right)\left(\left(A_{22} - \frac{dn^2}{l^2}\right)\left(A_{33} - \frac{dn^2}{l^2}\right) - A_{32}A_{23}\right),
\end{aligned}
$$

where $B_{0,1}$ depend on ϕ through $\mathscr{M}$.

Any given equilibrium of (3.1) will be locally stable if for every wave number $n \geq 0$ the roots of the characteristic equation (3.7) are all in the left half complex plane. With the above theorem established, we can present the following lemma. This idea follows from Gourley and Bartuccelli [9].

LEMMA 3.1. *For any given equilibrium of* (3.1), *the number of roots of the characteristic equation* (3.7) *in the right half complex plane equals*

$$\lim_{R \to \infty} \left(\frac{3}{2} - \frac{1}{\pi} arg \Phi(iR, n^2, q) \right). \tag{3.8}$$

The proof is shown in the appendix. With the above lemma, we can now establish the following theorem.

THEOREM 3.2. *All roots of the characteristic equation* (3.7) *have negative real part if* $\Phi(0, n^2, q) < 0$, $Im\Phi'(0, n^2, q) < 0$, *and there exists an* $x_0 \in (0, \infty)$ *such that* $Re\Phi'(x_0, n^2, q) = 0$ *and* $Re\Phi(x_0, n^2, q) > 0$, *where the prime is the derivative with respect to* R.

Proof. To get the local stability for the system (3.1), we need to prove that

$$\lim_{R \to \infty} arg \Phi(iR, n^2, q) = \frac{3\pi}{2}. \tag{3.9}$$

In view of (3.7), we have

$$\Phi(iR, n^2, q) = R^3 i - B_2(n^2, q)R^2 + B_1(iR, n^2, q)iR + B_0(iR, n^2, q) = 0.$$

For large value of R,

$$\text{Re}\Phi(iR, n^2, q) \sim -B_2(n^2, q)R^2, \qquad \text{Im}\Phi(iR, n^2, q) \sim R^3.$$

Also, when $R = 0$,

$$\Phi(0, n^2, q) = B_0(0, n^2, q).$$

The sign of $\Phi(0, n^2, q)$ determines whether the complex number $\Phi(iR, n^2, q)$ starts on the positive or the negative real axis when $R = 0$. The sign of $B_2(n^2, q)$ determines whether $\Phi(iR, n^2, q)$ ends up in the first or the second quadrant as $R \to \infty$. From the assumption that $\Phi(0, n^2, q) < 0$, the complex number $\Phi(iR, n^2, q)$ has the following two cases. (I) When $B_2(n^2, q) < 0$, $\Phi(iR, n^2, q)$ starts on the negative real axis and ends up in the first quadrant. (II) When $B_2(n^2, q) > 0$, the existence of x_0 guarantees that $\text{Re}(iR, n^2, q)$ changes its monotonicity at x_0, which implies that $\Phi(iR, n^2, q)$ starts on the negative real axis and ends up in the second quadrant.

For the above two cases we show in Figure 2 some qualitative sketches of graphs that correspond to three different values of $\lim_{R \to \infty} arg \Phi(iR, n^2, q)$. Only the green curve is consistent with all the assumptions, which leads to (3.9). □

If $\Phi(0, n^2, q) = 0$, then Theorem 3.2 above does not apply, and 0 is a root of (3.7). We can determine the signs of the rest of the roots as follows. Suppose that 0 is root of order 1 of (3.7). Then we can write (3.7) as

$$\Phi(\phi, n^2, q) = -\phi \hat{\Phi}(\phi, n^2, q) = -\phi(\phi^2 - B_2(n^2, q)\phi - \hat{B}_1(\phi, n^2, q)),$$

where $\hat{B}_1(\phi, n^2, q) = B_1(\phi, n^2, q) - B_0(\phi, n^2, q)/\phi$. Notice that $\hat{B}_1(\phi, n^2, q)$ is analytic at 0 and $\hat{B}_1(0, n^2, q) \neq 0$. Thus the rest of the roots of (3.7) satisfy

$$\hat{\Phi}(\phi, n^2, q) = \phi^2 - B_2(n^2, q)\phi - \hat{B}_1(\phi, n^2, q) = 0. \tag{3.10}$$

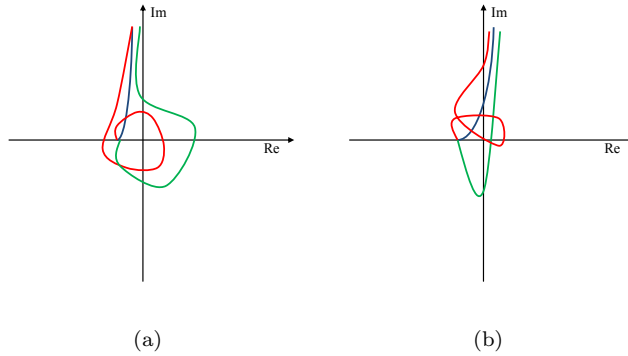From Gourley and Bartuccelli [9] we have the following lemma.

FIG. 2. *Possible qualitative sketches for case* (I) *and case* (II). *Green:*$\frac{3\pi}{2}$, *blue:*$-\frac{\pi}{2}$, *red:*$-\frac{5\pi}{2}$.

LEMMA 3.3. *The number of roots of the characteristic equation* (3.10) *in the right half complex plane equals*

$$(3.11) \qquad \lim_{R\to\infty}\left(1-\frac{1}{\pi}arg\hat{\Phi}(iR,n^2,q)\right).$$

THEOREM 3.4. *All the roots of* (3.10) *have negative real parts if*

$$\hat{\Phi}(0,n^2,q) > 0, \ \mathrm{Im}(\hat{\Phi}(iR,n^2,q)) \to \infty \ as \ R \to \infty, \ \mathrm{Im}(\hat{\Phi}'(0,n^2,q) > 0$$

or

$$\hat{\Phi}(0,n^2,q) < 0, \ \mathrm{Im}(\hat{\Phi}(iR,n^2,q)) \to -\infty \ as \ R \to \infty, \ \mathrm{Im}(\hat{\Phi}'(0,n^2,q) < 0.$$

Proof. Note that $\mathrm{Re}(\hat{\Phi}(iR,n^2,q)) \to -\infty$ as $R \to \infty$ and $\mathrm{Im}(\hat{\Phi}(iR,n^2,q)) \sim B_2(n^2,q)R$ as $R \to \infty$. Hence $\arg(\hat{\Phi}(iR,n^2,q))$ tends to either π or $-\pi$ as $R \to \infty$. The rest of the proof, which is similar to that of Theorem 3.2, shows that the given conditions guarantee

$$\lim_{R\to\infty} arg\hat{\Phi}(iR,n^2,q) = \pi. \qquad\qquad \square$$

3.2. Local stability of the diffusive NPZ model. In this subsection, we study the local stability of the uniform equilibria of (2.1). To investigate the linearized stability of (2.1), we set $N = N^* + u, P = P^* + v, Z = Z^* + w$, substitute into (2.1), and retain only linear terms in $u, v,$ and w, giving

(3.12)

$$\begin{cases} u_t(x,t) = du_{xx} - \mu P^* f'(N^*)u - \mu f(N^*)v \\ \qquad + \delta\int_{-\infty}^t\int_0^{l\pi} G(x,y,t-s)m_2(t-s)w(y,s)\mathrm{d}y\mathrm{d}s \\ \qquad + \lambda\int_{-\infty}^t\int_0^{l\pi} G(x,y,t-s)m_1(t-s)v(y,s)\mathrm{d}y\mathrm{d}s \\ \qquad + (1-r)gZ^*h'(P^*)\int_{-\infty}^t\int_0^{l\pi} G(x,y,t-s)m_3(t-s)v(y,s)\mathrm{d}y\mathrm{d}s \\ \qquad + (1-r)gh(P^*)\int_{-\infty}^t\int_0^{l\pi} G(x,y,t-s)m_3(t-s)w(y,s)\mathrm{d}y\mathrm{d}s, \\ v_t(x,t) = dv_{xx} + \mu P^* f'(N^*)u + (\mu f(N^*) - gZ^*h'(P^*) - \lambda)v - gh(P^*)w, \\ w_t(x,t) = dw_{xx} + rgZ^*h'(P^*)v + (rgh(P^*) - \delta)w \end{cases}$$

for all $x \in (0, l\pi)$. The Jacobian matrix of (2.1) at the equilibrium (N^*, P^*, Z^*) is

$$
J = \begin{bmatrix}
-\mu P^* f'(N^*) - \dfrac{dn^2}{l^2} & -\mu f(N^*) + \lambda \mathscr{M}_1 + (1-r)gh'(P^*)Z^* \mathscr{M}_3 & \delta \mathscr{M}_2 + (1-r)gh(P^*)\mathscr{M}_3 \\
\mu P^* f'(N^*) & \mu f(N^*) - \lambda - gh'(P^*)Z^* - \dfrac{dn^2}{l^2} & -gh(P^*) \\
0 & rgh'(P^*)Z^* & rgh(P^*) - \delta - \dfrac{dn^2}{l^2}
\end{bmatrix}.
$$

The characteristic equation is

$$
(3.13) \qquad \Phi(\phi, n^2, q) := -\phi^3 + \beta_2(n^2, q)\phi^2 + \beta_1(\phi, n^2, q)\phi + \beta_0(\phi, n^2, q) = 0,
$$

where $\beta_{1,0}$ depend on $\mathscr{M}_{1,2,3}$.

To compare with local stability in the closed NPZ model with no diffusion, we first recall two results from [17].

LEMMA 3.5. *Consider the model* (2.1) *with* $d = 0$, *and assume* (2.10) *and* (2.11). *Then*

- E_1 *is stable if* $N_T < f^{-1}(\frac{\lambda}{\mu})$,
- E_2 *is stable if* $f^{-1}(\frac{\lambda}{\mu}) + \frac{2\lambda(1+T_1\lambda)}{\mu f'(N^*)} \leq N_T < f^{-1}(\frac{\lambda}{\mu}) + (1+T_1\lambda)h^{-1}(\frac{\delta}{rg})$.

In addition, [17] showed that the local stability of E_3 under a specific delay kernel. To make the results more complete, we study the local stability with delay (2.2) and no diffusion.

LEMMA 3.6. *Consider the model* (2.1) *with* $d = 0$, *and assume* (2.12) *and* (2.14). E_3 *is locally stable if*

$$
(3.14) \qquad\qquad h'(P_3) \geq h(P_3)/P_3.
$$

Proof. When $d = 0$, for the nontrivial equilibrium (N_3, P_3, Z_3), the Jacobian matrix is

$$
J_0 = \begin{bmatrix}
-G_{11} & G_{12} + \lambda \mathscr{M}_1(\phi) + G_{13}\mathscr{M}_3(\phi) & \delta \mathscr{M}_2(\phi) + G_{14}\mathscr{M}_3(\phi) \\
G_{11} & G_{21} & G_{22} \\
0 & G_{31} & 0
\end{bmatrix}
$$

with

$$
G_{11} = \mu P_3 f'(N_3), \quad G_{12} = -\mu f(N_3), \quad G_{13} = (1-r)gh'(P_3)Z_3, \quad G_{14} = (1-r)gh(P_3),
$$
$$
G_{21} = \mu f(N_3) - \lambda - gh'(P_3)Z_3, \quad G_{22} = -gh(P_3), \quad G_{31} = rgh'(P_3)Z_3.
$$

The characteristic equation of the linearization around (N_3, P_3, Z_3) is then

$$
(3.15) \qquad \Phi_0(\phi, 0, q) := -\phi^3 + \hat{Y}_2(0, q)\phi^2 + \hat{Y}_1(\phi, 0, q)\phi + \hat{Y}_0(\phi, 0, q) = 0,
$$

where

$$
\hat{Y}_2(0, q) = G_{21} - G_{11},
$$
$$
\hat{Y}_1(\phi, 0, q) = G_{11}(\lambda \mathscr{M}_1(\phi, 0) + G_{13}\mathscr{M}_3(\phi, 0) + G_{12} + G_{21}) + G_{22}G_{31} < 0,
$$
$$
\hat{Y}_0(\phi, 0, q) = G_{11}G_{31}(G_{22} + \delta \mathscr{M}_2(\phi, 0) + G_{14}\mathscr{M}_3(\phi, 0)).
$$

Since $\Phi_0(0, 0, q) = \hat{Y}_0(0, 0, q) = G_{11}G_{31}(G_{22} + \delta + G_{14}) = 0$, 0 is a root of (3.15). Therefore, (3.15) can be written as

$$\Phi_0(\phi, 0, q) = \phi \hat{\Phi}_0(\phi, 0, q) = 0.$$

Notice that $\hat{\Phi}_0(0, 0, q) = \hat{Y}_1(0, 0, q) < 0$.

When $\phi = iR$, we have

(3.16)
$$\hat{\Phi}_0(iR, 0, q) = R^2 + \hat{Y}_2(0, q)Ri + \bar{Y}_1(iR, 0, q),$$

where $\bar{Y}_1(iR, n^2, q)) = \hat{Y}_1(iR, n^2, q) - \hat{Y}_0(iR, n^2, q)/iR$. Then, under the assumption (3.14), we have

$$\hat{Y}_2(0, q) = \frac{\delta Z_3}{r P_3}\left(1 - \frac{h'(P_3)}{h(P_3)}P_3\right) - \mu P_3 f'(N_3) < 0,$$

which implies that $\lim_{R \to \infty} \mathrm{Im}(\hat{\Phi}_0(iR, n^2, q)) = -\infty$. Besides, it's clear that $\mathrm{Im}\Phi_0'(0, 0, q) < 0$. The result then follows from Theorem 3.4. □

In the following, we study the local stability of the equilibria of model (2.1) when $d > 0$.

THEOREM 3.7. *Assume that $\mu f(N_T) - \lambda < 0$; then the trivial equilibrium $(N_T, 0, 0)$ of* (2.1) *is locally stable.*

Proof. For the trivial solution $(N_T, 0, 0)$, the Jacobian matrix is

$$J_1 = \begin{bmatrix} -\dfrac{dn^2}{l^2} & -\mu f(N_T) + \lambda \mathscr{M}_1(\phi) & \delta \mathscr{M}_2(\phi) \\ 0 & \mu f(N_T) - \lambda - \dfrac{dn^2}{l^2} & 0 \\ 0 & 0 & -\delta - \dfrac{dn^2}{l^2} \end{bmatrix}.$$

The characteristic equation of the linearization around $(N_T, 0, 0)$ is then

(3.17)
$$\Phi_1(\phi, n^2, q) := \left(-\frac{dn^2}{l^2} - \phi\right)\left(-\delta - \frac{dn^2}{l^2} - \phi\right)\left(\mu f(N_T) - \lambda - \frac{dn^2}{l^2} - \phi\right) = 0.$$

It is clear that the roots of (3.17) are

$$-\frac{dn^2}{l^2}, \quad -\delta - \frac{dn^2}{l^2}, \quad \mu f(N_T) - \lambda - \frac{dn^2}{l^2}.$$

Thus, under the conditions of the theorem all roots are negative if $n > 0$. If $n = 0$ there is one zero root and the rest are negative. □

THEOREM 3.8. *Assume that* (2.10) *and* (2.11) *are satisfied and*

(3.18)
$$rgh(P_2) - \delta < 0;$$

then the trivial equilibrium $(N_2, P_2, 0)$ of (2.1) *is locally stable.*

Proof. For the trivial equilibrium $(N_2, P_2, 0)$, the Jacobian matrix is

(3.19)
$$J_2 = \begin{bmatrix} -\mu P_2 f'(N_2) - \dfrac{dn^2}{l^2} & -\lambda + \lambda \mathscr{M}_1(\phi) & \delta \mathscr{M}_2(\phi) + (1-r)gh(P_2)\mathscr{M}_3(\phi) \\ \mu P_2 f'(N_2) & -\dfrac{dn^2}{l^2} & -gh(P_2) \\ 0 & 0 & rgh(P_2) - \delta - \dfrac{dn^2}{l^2} \end{bmatrix}.$$

The characteristic equation of the linearization around $(N_2, P_2, 0)$ is then

$$(3.20) \qquad \Phi_2(\phi, n^2, q) := -\phi^3 + C_2(n^2, q)\phi^2 + C_1(\phi, n^2, q)\phi + C_0(\phi, n^2, q) = 0,$$

where

$$C_2(n^2, q) = D_{33} - D_{11} - \frac{3dn^2}{l^2},$$

$$C_0(\phi, n^2, q) = \left(D_{33} - \frac{dn^2}{l^2}\right)\left[\lambda D_{11}(1 - \mathscr{M}_1) + \frac{dn^2}{l^2}\left(D_{11} + \frac{dn^2}{l^2}\right)\right],$$

$$C_1(\phi, n^2, q) = \lambda D_{11}(\mathscr{M}_1 - 1) + D_{11}D_{33} + 2(D_{33} - D_{11})\frac{dn^2}{l^2} - \frac{3d^2n^4}{l^4}$$

with

$$D_{11} = \mu P_2 f'(N_2), \quad D_{13} = (1-r)gh(P_2), \quad D_{23} = -gh(P_2), \quad D_{33} = rgh(P_2) - \delta.$$

For $n = 0$, the roots of (3.20) are as described in Lemma 3.5. Now consider $n > 0$. By (3.4), we have $\mathscr{M}_1 = \mathscr{C}_1(R) - \mathscr{S}_1(R)i$, and

$$(3.21) \qquad \Phi_2(iR, n^2, q) = \mathrm{Re}\Phi_2(iR, n^2, q) + \mathrm{Im}\Phi_2(iR, n^2, q)i,$$

where

$$\mathrm{Re}\Phi_2(iR, n^2, q) = -\left(D_{33} - D_{11} - \frac{3dn^2}{l^2}\right)R^2 + \lambda D_{11}\mathscr{S}_1(R)R + o(1),$$

$$\mathrm{Im}\Phi_2(iR, n^2, q) = R^3 + \left(D_{11}(\lambda\mathscr{C}_1(R) - \lambda + D_{33}) + 2(D_{33} - D_{11})\frac{dn^2}{l^2} - \frac{3d^2n^4}{l^4}\right)R$$
$$+ \lambda D_{11}\left(D_{33} - \frac{dn^2}{l^2}\right)\mathscr{S}_1(R).$$

One easily concludes from (3.21) that, for large values of R,

$$\mathrm{Re}\Phi_2(iR, n^2, q) \sim constant\ R^2, \quad \mathrm{Im}\Phi_2(iR, n^2, q) \sim R^3.$$

Also, when $R = 0$,

$$\Phi_2(0, n^2, q) = \left(rgh(P_2) - \delta - \frac{dn^2}{l^2}\right)\left(\mu P_2 f'(N_2)\left(\lambda - \lambda\mathscr{C}(0) + \frac{dn^2}{l^2}\right) + \frac{d^2n^4}{l^4}\right).$$

Since $\lambda - \lambda\mathscr{C}(0) \geq 0$, it is obvious that under the assumption (3.18),

$$\Phi_2(0, n^2, q) \leq \frac{dn^2}{l^2}\left(rgh(P_2) - \delta - \frac{dn^2}{l^2}\right)\left(\mu P_2 f'(N_2) + \frac{dn^2}{l^2}\right) < 0.$$

In the view of (3.21),

$$\mathrm{Im}\Phi_2'(iR, n^2, q) = 3R^2 + W_{20}\mathscr{C}_1'(R)R + W_{21}\mathscr{S}_1'(R) + W_{22},$$

where

$$W_{20} = \lambda D_{11}, \quad W_{21} = \lambda D_{11}\left(D_{33} - \frac{dn^2}{l^2}\right),$$

$$W_{22} = D_{11}(\lambda\mathscr{C}_1(R) - \lambda + D_{33}) + 2(D_{33} - D_{11})\frac{dn^2}{l^2} - \frac{3d^2n^4}{l^4}.$$

Note that $D_{11} > 0$ and, under the assumption (3.18), $D_{33} < 0$. Thus we have $W_{20} > 0$ and $W_{22} < 0, W_{21} < 0$. Then, for every wave number $n=1,2\ldots$,

$$\mathrm{Im}\Phi_2'(0, n^2, q) = W_{22} + W_{21}\mathscr{S}_1'(0) < W_{22} + W_{21}T_{f_1} < 0.$$

Further, $\lim_{R\to\infty} \mathrm{Im}\Phi_2'(iR, n^2, q) \to \infty$ and $\lim_{R\to\infty}\mathrm{Re}\Phi_2(iR, n^2, q) \to \infty$. Therefore, the result follows from Theorem 3.2 and Lemma 3.5. $\qquad\square$

THEOREM 3.9. *Assume that* (2.12) *is satisfied and that* $Z_3 > 0$ *and assume* (3.14); *then the nontrivial equilibrium* (N_3, P_3, Z_3) *of system* (2.1) *is locally stable.*

Proof. For the nontrivial equilibrium (N_3, P_3, Z_3), the Jacobian matrix is

$$J_3 = \begin{bmatrix} -G_{11} - \dfrac{dn^2}{l^2} & G_{12} + \lambda\mathscr{M}_1(\phi) + G_{13}\mathscr{M}_3(\phi) & \delta\mathscr{M}_2(\phi) + G_{14}\mathscr{M}_3(\phi) \\[2mm] G_{11} & G_{21} - \dfrac{dn^2}{l^2} & G_{22} \\[2mm] 0 & G_{31} & -\dfrac{dn^2}{l^2} \end{bmatrix}.$$

The characteristic equation of the linearization around (N_3, P_3, Z_3) is then

(3.22) $\qquad \Phi_3(\phi, n^2, q) := -\phi^3 + Y_2(n^2, q)\phi^2 + Y_1(\phi, n^2, q)\phi + Y_0(\phi, n^2, q) = 0,$

where

$$Y_2(n^2, q) = \hat{Y}_2(0, q) - 3\frac{dn^2}{l^2}, \quad Y_1(\phi, n^2, q) = \hat{Y}_1(\phi, 0, q) + \frac{2dn^2}{l^2}\hat{Y}_2(0, q) - \frac{3d^2n^4}{l^4},$$

$$Y_0(\phi, n^2, q) = \hat{Y}_0(\phi, 0, q) + \frac{dn^2}{l^2}(G_{22}G_{31} + G_{11}(G_{12} + G_{21} + \lambda\mathscr{M}_1 + G_{13}\mathscr{M}_3))$$
$$+ \frac{d^2n^4}{l^4}\hat{Y}_2(0, q) - \frac{d^3n^6}{l^6}.$$

For $n = 0$, the roots of (3.22) are as described in Lemma 3.6. Now consider $n > 0$. When $\phi = iR$, we have

(3.23) $\qquad \Phi_3(iR, n^2, q) = \mathrm{Re}\Phi_3(iR, n^2, q) + \mathrm{Im}\Phi_3(iR, n^2, q)i,$

where

$$\mathrm{Re}\Phi_3(iR, n^2, q) = -Y_2(n^2, q)R^2 + o(1)R + o(1),$$
$$\mathrm{Im}\Phi_3(iR, n^2, q) = R^3 + W_{31}R + W_{30}$$

with

$$W_{31} = G_{22}G_{31} + \frac{2dn^2}{l^2}\hat{Y}_2(0, q) - \frac{3d^2n^4}{l^4} + G_{11}(G_{12} + G_{21} + G_{13}\mathscr{C}_3(R) + \lambda\mathscr{C}_1(R)),$$

$$W_{30} = -G_{11}\left(\frac{dn^2}{l^2}(\lambda\mathscr{S}_1(R) + G_{13}\mathscr{S}_3(R)) + G_{31}(\lambda\mathscr{S}_2(R) + G_{14}\mathscr{S}_3(R))\right).$$

One easily concludes from (3.21) that, for large values of R,

$$\mathrm{Re}\Phi_3(iR, n^2, q) \sim constant\ R^2, \quad \mathrm{Im}\Phi_3(iR, n^2, q) \sim R^3.$$

Also, when $R = 0$,

$$\Phi_3(0, n^2, q) = G_{11}G_{31}(G_{22} + \delta\mathscr{C}_2(R) + G_{14}\mathscr{C}_3(R)) + \frac{dn^2}{l^2}(G_{22}G_{31} + G_{11}(G_{12} + G_{21}$$
$$+ \lambda\mathscr{C}_1(R) + G_{13}\mathscr{C}_3)(R)) + \frac{d^2n^4}{l^4}\hat{Y}_2(0, q) - \frac{d^3n^6}{l^6}.$$

By calculation, we have

(3.24) $G_{12} + G_{21} + \lambda\mathscr{C}_1(R) + G_{13}\mathscr{C}_3(R) < 0, \quad G_{22} + \delta\mathscr{C}_2(R) + G_{14}\mathscr{C}_3(R) \leq 0.$

According to (3.24) and (3.14), $\Phi_3(0, n^2, q) < 0$. Besides, in the view of (3.23),

$$\text{Im}\Phi_3'(iR, n^2, q) = 3R^2 + W_{40}R + W_{41} + W_{42},$$

where

$$W_{40} = G_{11}(\lambda\mathscr{C}_1'(R) + G_{13}\mathscr{C}_3'(R)) > 0,$$
$$W_{41} = -G_{11}\left(\frac{dn^2}{l^2}(\lambda\mathscr{S}_1'(R) + G_{13}\mathscr{S}_3'(R)) + G_{31}(\lambda\mathscr{S}_2'(R) + G_{14}\mathscr{S}_3'(R))\right) < 0,$$
$$W_{42} = G_{22}G_{31} + \frac{2dn^2}{l^2}\hat{Y}_2(0, q) - \frac{3d^2n^4}{l^4} + G_{11}(G_{12} + G_{21} + G_{13}\mathscr{C}_3(R) + \lambda\mathscr{C}_1(R)) < 0.$$

Then, for every wave number $n = 1, 2, \ldots$, $\text{Im}\Phi_3'(0, n^2, q) = W_{42} + W_{41} < 0$, and $\lim_{R\to\infty}\text{Im}\Phi_3'(iR, n^2, q) = \infty$. Besides, $\lim_{R\to\infty}\text{Re}\Phi_3(iR, n^2, q) = \infty$. The result then follows from Theorem 3.2 and Lemma 3.6.   □

Remark 3.10. If $h'(P_3) < h(P_3)/P_3$, we see that if Z_3 is sufficiently small, the term $G_{21} - G_{11}$ also is negative and (N_3, P_3, Z_3) is therefore locally stable.

Remark 3.11. The conditions of Theorem 3.9 only guarantee stability of the equilibrium $E_3 = (N_3, P_3, Z_3)$ as the characteristic equation has a zero root of multiplicity one. This root is due to the fact that the equilibrium E_3 is not isolated but comes in a set parameterized by N_T. The zero root corresponds to perturbations along this set. Given any appropriate initial data for the model, N_T will be fixed and so will the corresponding unique value of E_3. Thus under the conditions of Theorem 3.9 any solution will asymptotically limit on the value of E_3 determined by N_T for the solution. A similar remark applies to Theorems 3.7 and 3.8.

4. Global behavior of the uniform equilibria. In this section, the global stability of the uniform equilibria of the system (2.1) is studied. The results are carried out for the case when $m_i(t) = \frac{1}{\tau}e^{-\frac{t}{\tau}}, i = 1, 2, 3$. The use of this particular delay kernel enables us to reformulate system (2.1) as a reaction-diffusion system without delay terms (the delay parameter appears as a coefficient in the reformulated system). This is particularly useful for the purposes of numerical simulation.

It is useful to define the following component, which can be thought of the detritus in the system:

$$Q(x, t) = \int_{-\infty}^{t}\int_{0}^{l\pi}G(x, y, t - s)e^{-\frac{t-s}{\tau}}(\lambda P(y, s) + \delta Z(y, s)$$
$$+ (1 - r)gZ(y, s)h(P(y, s)))dyds.$$

It is then easy to see that system (2.1) is equivalent to the following system for $t > 0, x \in (0, l\pi)$:

(4.1)

$$\begin{cases} N_t(x,t) = dN_{xx}(x,t) - \mu P(x,t)f(N(x,t)) + \frac{1}{\tau}Q(x,t), \\ P_t(x,t) = dP_{xx}(x,t) + \mu P(x,t)f(N(x,t)) - gZ(x,t)h(P(x,t)) - \lambda P(x,t), \\ Z_t(x,t) = dZ_{xx}(x,t) + rgZ(x,t)h(P(x,t)) - \delta Z(x,t), \\ Q_t(x,t) = dQ_{xx}(x,t) + \lambda P(x,t) + \delta Z(x,t) + (1-r)gZ(x,t)h(P(x,t) - \frac{1}{\tau}Q(x,t) \end{cases}$$

with homogeneous Neumann boundary conditions and the initial conditions for $t \in [-\infty, 0], x \in [0, l\pi]$,

$$N(x,0) = N_0(x) \geq 0, \ P(x,0) = P_0(x) \geq 0, \ Z(x,0) = Z_0(x) > 0,$$

$$Q(x,0) = \int_{-\infty}^0 \int_0^{l\pi} G(x,y,-s)e^{\frac{s}{\tau}}(\lambda P(y,s) + \delta Z(y,s)$$
$$+ (1-r)gZ(y,s)h(P(y,s)))\mathrm{d}y\mathrm{d}s \geq 0.$$

Adding the equations in (4.1) and integrating x on the interval $(0, l\pi)$ yields

$$\int_0^{l\pi} (P_t(x,t) + N_t(x,t) + Z_t(x,t) + Q_t(x,t))\mathrm{d}x$$
$$= \frac{\partial}{\partial t} \int_0^{l\pi} (P(x,t) + N(x,t) + Z(x,t) + Q(x,t))\mathrm{d}x = 0,$$

which leads to the conservation law

(4.2)
$$\int_0^{l\pi} (P(x,t) + N(x,t) + Z(x,t) + Q(x,t))\mathrm{d}x = \tilde{N}_T.$$

Thus, for a spatially homogeneous equilibrium solution, (N^*, P^*, Z^*, Q^*), the conservation law (4.2) can be written as

(4.3)
$$N_T = \frac{\tilde{N}_T}{l\pi} = P^* + N^* + Z^* + Q^*.$$

Then, using the conservation law (4.3), the equilibria of (4.1) are given by

$$E_1^*(N_1^*, P_1^*, Z_1^*, Q_1^*) = (N_T, 0, 0, 0),$$
$$E_2^*(N_2^*, P_2^*, Z_2^*, Q_2^*) = \left(f^{-1}\left(\frac{\lambda}{\mu}\right), \frac{N_T - N_2^*}{1 + \lambda\tau}, 0, \lambda\tau P_2^* \right), \text{ and}$$
$$E_3^*(N_3^*, P_3^*, Z_3^*, Q_3^*) = \left(N_3^*, h^{-1}\left(\frac{\delta}{rg}\right), \frac{(\mu f(N_3^*) - \lambda)P_3^* r}{\delta}, \tau\mu P_3^* f(N_3^*) \right),$$

where N_3^* satisfies the following implicit expression:

$$N_T = N_3^* + P_3^* + Z_3^* + \tau\mu P_3^* f(N_3^*).$$

Here, E_2^* exists if and only if (2.10) and (2.11) hold, and E_3^* exists if and only if (2.12) holds.

Next, we use the method of upper and lower solutions for mixed quasi-monotone functions ([21, Definition 2.1]) to show the existence of a classical solution to (4.1).

THEOREM 4.1. *System (4.1) has a unique solution $(N(x,t), P(x,t), Z(x,t), Q(x,t))$ such that $0 < N(x,t) < \tilde{N}_T, \ 0 < P(x,t) < \tilde{N}_T, \ 0 < Z(x,t) < \tilde{N}_T, \ 0 < Q(x,t) < \tilde{N}_T$ for $t \in (0,\infty)$ and $x \in [0, l\pi]$.*

Proof. We begin by defining

$$g_1(x,t) = \frac{1}{\tau}Q - \mu P f(N), g_2(x,t) = \mu P f(N) - gZh(P) - \lambda P,$$

$$g_3(x,t) = rgZh(P) - \delta Z, g_4(x,t) = \lambda P + \delta Z + (1-r)gZh(P) - \frac{1}{\tau}Q.$$

Since, in $\overline{\mathbb{R}^4_+} = \{N \geq 0, P \geq 0, Z \geq 0, Q \geq 0\}$,

$$\frac{\partial g_1}{\partial P} = -\mu f(N) < 0, \quad \frac{\partial g_1}{\partial Z} = 0, \quad \frac{\partial g_1}{\partial Q} = \frac{1}{\tau} > 0,$$

$$\frac{\partial g_2}{\partial N} = \mu P f'(N) > 0, \quad \frac{\partial g_2}{\partial Z} = -gh(P) < 0, \quad \frac{\partial g_2}{\partial Q} = 0,$$

$$\frac{\partial g_3}{\partial N} = 0 \quad \frac{\partial g_3}{\partial P} = rgZh'(P) > 0, \quad \frac{\partial g_3}{\partial Q} = 0,$$

$$\frac{\partial g_4}{\partial N} = 0, \quad \frac{\partial g_4}{\partial P} = \lambda + (1-r)gZh'(P) > 0, \quad \frac{\partial g_4}{\partial Z} = \delta + (1-r)gh(P) > 0,$$

and then (4.1) is a mixed quasi-monotone system. Let $(\hat{N}(x,t), \hat{P}(x,t), \hat{Z}(x,t), \hat{Q}(x,t)) = (0,0,0,0)$ and $(\tilde{N}(x,t), \tilde{P}(x,t), \tilde{Z}(x,t), \tilde{Q}(x,t)) = (\tilde{N}^*(t), \tilde{P}^*(t), \tilde{Z}^*(t), \tilde{Q}^*(t))$, where $(\tilde{N}^*(t), \tilde{P}^*(t), \tilde{Z}^*(t), \tilde{Q}^*(t))$ is the unique solution of

(4.4)
$$\begin{cases} \dfrac{\mathrm{d}N}{\mathrm{d}t} = \dfrac{1}{\tau}Q, \\ \dfrac{\mathrm{d}P}{\mathrm{d}t} = (\mu f(N) - \lambda)P, \\ \dfrac{\mathrm{d}Z}{\mathrm{d}t} = (rgh(P) - \delta)Z, \\ \dfrac{\mathrm{d}Q}{\mathrm{d}t} = \delta Z + \lambda P + (1-r)gZh(P) - \dfrac{1}{\tau}Q, \\ N(0) = \sup_{[0,l\pi]} N_0(x), \quad P(0) = \sup_{[0,l\pi]} P_0(x), \quad Z(0) = \sup_{[0,l\pi]} Z_0(x), \quad Q(0) = \sup_{[0,l\pi]} Q_0(x). \end{cases}$$

Then $(\hat{N}(x,t), \hat{P}(x,t), \hat{Z}(x,t), \hat{Q}(x,t))$ and $(\tilde{N}(x,t), \tilde{P}(x,t), \tilde{Z}(x,t), \tilde{Q}(x,t))$ are the lower solution and upper solution to (4.1), since

$$\begin{cases} \dfrac{\partial \tilde{N}(x,t)}{\partial t} - \tilde{N}_{xx} - g_1(\tilde{N}(x,t), \hat{P}(x,t), \hat{Z}(x,t), \tilde{Q}(x,t)) = \mu f(N^*(t)) > 0, \\ \dfrac{\partial \tilde{P}(x,t)}{\partial t} - \tilde{P}_{xx} - g_2(\tilde{N}(x,t), \tilde{P}(x,t), \hat{Z}(x,t), \hat{Q}(x,t)) = gZ^*(t)h(P^*(t)) > 0, \\ \dfrac{\partial \tilde{Z}(x,t)}{\partial t} - \tilde{Z}_{xx} - g_3(\hat{N}(x,t), \tilde{P}(x,t), \tilde{Z}(x,t), \hat{Q}(x,t)) = 0, \\ \dfrac{\partial \tilde{Q}(x,t)}{\partial t} - \tilde{Q}_{xx} - g_4(\hat{N}(x,t), \tilde{P}(x,t), \tilde{Z}(x,t), \tilde{Q}(x,t)) = 0, \end{cases}$$

and

$$\begin{cases} \dfrac{\partial \hat{N}(x,t)}{\partial t} - d\hat{N}_{xx} - g_1(\hat{N}(x,t), \tilde{P}(x,t), \tilde{Z}(x,t), \hat{Q}(x,t)) = 0, \\ \dfrac{\partial \hat{P}(x,t)}{\partial t} - d\hat{P}_{xx} - g_2(\hat{N}(x,t), \hat{P}(x,t), \tilde{Z}(x,t), \tilde{Q}(x,t)) = 0, \\ \dfrac{\partial \hat{Z}(x,t)}{\partial t} - d\hat{Z}_{xx} - g_3(\tilde{N}(x,t), \hat{P}(x,t), \hat{Z}(x,t), \tilde{Q}(x,t)) = 0, \\ \dfrac{\partial \hat{Q}(x,t)}{\partial t} - d\hat{Q}_{xx} - g_4(\tilde{N}(x,t), \hat{P}(x,t), \hat{Z}(x,t), \hat{Q}(x,t)) = 0. \end{cases}$$

Also, the boundary conditions and the initial conditions are satisfied. For any (N_a, P_a, Z_a, Q_a) and (N_b, P_b, Z_b, Q_b) in X_T, it is clear that

$$|g_i(N_a, P_a, Z_a, Q_a) - g_i(N_b, P_b, Z_b, Q_b)| \leq K_1(|N_a - N_b| + |P_a - P_b| + |Z_a - Z_b| + |Q_a - Q_b|),$$

where $K_i = K_i(x,t)(i = 1, 2, 3, 4)$. Therefore, Lemma 2.1 in [21] shows that (4.1) has a unique globally defined solution $(N(x,t), P(x,t), Z(x,t), Q(x,t))$, which satisfies

$$0 \leq N(x,t) \leq \tilde{N}^*(t), \quad 0 \leq P(x,t) \leq \tilde{P}^*(t), \quad 0 \leq Z(x,t) \leq \tilde{Z}^*(t),$$
$$0 \leq Q(x,t) \leq \tilde{Q}^*(t), \quad t \geq 0.$$

The strong maximum principle implies that $N(x,t), P(x,t), Z(x,t), Q(x,t) > 0$ when $t > 0$ for all $x \in [0, l\pi]$. Using the positivity of solutions, it follows from the conservation law (4.2) that $N(x,t), P(x,t), Z(x,t), Q(x,t)$ are bounded above by the total biomass, $\tilde{N}_T$. □

Remark 4.2. Consider the case where the delay distributions in system (2.1) are changed to higher order gamma distributions: $m_i(t) = \frac{t^{k-1}}{(k-1)!\tau^k} e^{-\frac{t}{\tau}}$ with $k > 1$ an integer. The model then becomes system (4.1) with the additional equations

$$Q_{j,t}(x,t) = dQ_{j,xx}(x,t) + \frac{1}{\tau}(Q_{j-1}(x,t) - Q_j(x,t)), \quad j = 1, \ldots, k-1.$$

The proof of Theorem 4.1 can be easily extended to this case.

We now give conditions for the global stability of E_1^*.

THEOREM 4.3. $E_1^* = (N_T, 0, 0, 0)$ *is global stable if*

$$(4.5) \qquad \qquad \mu f(N_T) - \lambda < 0.$$

Proof. First we show that under the assumption (4.5), $rgh(P(x,t)) - \delta < 0$. Using the system (4.1) and Theorem 4.1, we observe that $P(x,t)$ satisfies

(4.6)
$$\begin{cases} P_t(x,t) \leq dP_{xx} + \mu P f(N) - \lambda P < dP_{xx} + P(\mu f(N_T) - \lambda), & t > 0, \quad x \in (0, l\pi), \\ \dfrac{\partial P}{\partial x} = 0, & t > 0, \quad x = 0, l\pi. \end{cases}$$

Then from comparison principle of the parabolic equations, it is easy to verify that $P(x,t) < \check{P}(t)$, where $\check{P}(t)$ is the (spatially homogeneous) solution of

$$(4.7) \qquad \begin{cases} P_t(x,t) = dP_{xx} + (\mu f(N_T) - \lambda)P, & t > 0, \quad x \in (0, l\pi), \\ \dfrac{\partial P}{\partial x} = 0, & t > 0, \quad x = 0, l\pi, \\ P(0) = \sup P_0(x) & x \in [0, l\pi], \end{cases}$$

that is, $\check{P}(t) = P(0)e^{[\mu f(N_T) - \lambda]t} > 0$. From Theorem 4.1, $P(x,t) > 0$ we then have $\lim_{t \to \infty} P(x,t) = 0$ for $x \in [0, l\pi]$. It follows that there is a function, $\omega_1(t) = rgh\check{P}(t)$, such that $\lim_{t \to \infty, x \in [0, l\pi]} \omega_1(x,t) = 0$ and

$$(4.8) \qquad \begin{cases} Z_t(x,t) < dZ_{xx} + \omega_1 - \delta Z, & t > 0, \quad x \in (0, l\pi), \\ \dfrac{\partial Z}{\partial x} = 0, & t > 0, \quad x = 0, l\pi. \end{cases}$$

Then from the comparison principle, $Z(x,t) < \check{Z}(t)$, where $\check{Z}(t)$ is the solution of

$$
(4.9) \quad
\begin{cases}
Z_t(x,t) = dZ_{xx} + \omega_1 - \delta Z, & t > 0, \quad x \in (0, l\pi), \\
\dfrac{\partial Z}{\partial x} = 0, & t > 0, \quad x = 0, l\pi, \\
Z(0) = \sup Z_0(x) & x \in [0, l\pi],
\end{cases}
$$

that is, $\check{Z}(t) = e^{-\delta t} Z(0) + e^{-\delta t} \int_0^t e^{\delta u} \omega_1(u) \mathrm{d}u$. In the case where $\int_0^t e^{\delta u} \omega_1(u) \mathrm{d}u$ it is obvious the final term approaches zero as $t \to \infty$. Since $Z(x,t) > 0$ we then have $\lim_{t \to \infty} Z(x,t) = 0$ for $x \in [0, l\pi]$. Similarly, there exists a function $\omega_2(x,t) = \lambda \check{P}(t) + (\delta + (1-r)g)\check{Z}(t)$ such that $\lim_{t \to \infty, x \in [0, l\pi]} \omega_2(x,t) = 0$ and

$$
(4.10) \quad
\begin{cases}
Q_t(x,t) < dQ_{xx} + \omega_2 - \dfrac{1}{\tau}Q, & t > 0, \quad x \in (0, l\pi), \\
\dfrac{\partial Q}{\partial x} = 0, & t > 0, \quad x = 0, l\pi;
\end{cases}
$$

then from the comparison principle, $Q(x,t) < \check{Q}(t)$. Here, $\check{Q}(t)$ is the solution of

$$
(4.11) \quad
\begin{cases}
Q_t(x,t) = dQ_{xx} + \omega_2 - \dfrac{1}{\tau}Q, & t > 0, \quad x \in (0, l\pi), \\
\dfrac{\partial Q}{\partial x} = 0, & t > 0, \quad x = 0, l\pi, \\
Q(0) = \sup Q_0(x) & x \in [0, l\pi],
\end{cases}
$$

where $\check{Q}(t) = e^{-\frac{1}{\tau}t} Q(0) + e^{-\frac{1}{\tau}t} \int_0^t e^{\frac{1}{\tau}u} \omega_2(u) \mathrm{d}u$. As $t \to \infty$, the term $e^{-\frac{1}{\tau}t} \int_0^t e^{\frac{1}{\tau}u} \omega_2(u) \mathrm{d}u$ goes to 0. Since $Q(x,t) > 0$, we have $\lim_{t \to \infty} Q(x,t) = 0$, $x \in [0, l\pi]$. Then from the conservation law (4.3), we have $\lim_{t \to \infty} N(x,t) = N_T$, $x \in [0, l\pi]$. Therefore E_1^* is globally stable. $\qquad \square$

In the following, we discuss the Hopf bifurcation near E_3^*, using the Hopf bifurcation theorem for PDEs [16, 29]. Here, we choose d as a bifurcation parameter.

For the nontrivial solution E_3^*, the Jacobian matrix is

$$
J_3^* =
\begin{bmatrix}
-I_{11} - \dfrac{dn^2}{l^2} & I_{12} & 0 & \dfrac{1}{\tau} \\
I_{11} & I_{22} - \dfrac{dn^2}{l^2} & I_{23} & 0 \\
0 & I_{32} & -\dfrac{dn^2}{l^2} & 0 \\
0 & I_{42} & I_{43} & -\dfrac{1}{\tau} - \dfrac{dn^2}{l^2}
\end{bmatrix},
$$

where

$I_{11} = \mu P_3^* f'(N_3^*) > 0$, $I_{12} = -\mu f(N_3^*) < 0$, $I_{22} = \mu f(N_3^*) - \lambda - g Z_3^* h'(P_3^*)$,

$I_{23} = -\dfrac{\delta}{r} < 0$, $I_{32} = rg Z_3^* h'(P_3^*) > 0$, $I_{42} = \lambda + (1-r)g Z_3^* h'(P_3^*) > 0$, $I_{43} = \dfrac{\delta}{r} > 0$.

The characteristic equation is

$$
(4.12) \quad \Phi_3^*(\phi, n^2, q) =: \left(\dfrac{dn^2}{l^2} + \phi \right)(\phi^3 + \phi^2 e_2 + \phi e_1 + e_0) = 0,
$$

where

$$c_1 = \frac{I_{32}}{r}(\delta + I_{11}) + I_{11}\lambda + \frac{e_4}{\tau}, \; c_0 = \frac{I_{32}}{r}\left(\delta\left(I_{11} + \frac{1}{\tau}\right) + I_{11}\frac{r}{\tau}\right), \; e_2 = \frac{3dn^2}{l^2} + \frac{1}{\tau} + e_4,$$

$$e_1 = c_1 + \frac{3d^2n^4}{l^4} + \frac{2dn^2}{l^2}\left(\frac{1}{\tau} + e_4\right), \; e_0 = c_0 + \frac{dn^2}{l^2}\left(c_1 + \frac{dn^2}{l^2}\left(\frac{dn^2}{l^2} + \frac{1}{\tau} + e_4\right)\right),$$

$$e_4 = \mu P_3^* f'(N_3^*) - \mu f(N_3^*) + gZ_3^* h'(P_3^*) + \lambda.$$

Therefore we have the following theorem.

THEOREM 4.4. *Assume the equilibrium point E_3^* exists, that is, (2.12), (2.14) are satisfied. If $P_3^* \geq f(N_3^*)/f'(N_3^*)$, E_3^* undergoes a Hopf bifurcation at each $d > 0$ and $n \geq 1$ satisfying*

$$\frac{8d^3n^6}{l^6} + \frac{8d^2n^4}{l^4}\left(e_4 + \frac{1}{\tau}\right) + \frac{2dn^2}{l^2}\left(c_1 + \left(e_4 + \frac{1}{\tau}\right)^2\right) + c_1\left(e_4 + \frac{1}{\tau}\right) - c_0 = 0.$$

Proof. The inequality $P_3^* \geq f(N_3^*)/f'(N_3^*)$ guarantees that e_2, e_1 are positive. If f is a Type II response $f(N) = \frac{N}{N+k}$, then this condition can be satisfied for $h^{-1}(\frac{\delta}{rg}) \geq \frac{N_3^*(N_3^*+k)}{k}$. Further, it can be shown that $e_2e_1 = e_0$ when the bifurcation parameter d satisfies

(4.13)

$$\frac{8d^3n^6}{l^6} + \frac{8d^2n^4}{l^4}\left(e_4 + \frac{1}{\tau}\right) + \frac{2dn^2}{l^2}\left(c_1 + \left(e_4 + \frac{1}{\tau}\right)^2\right) + c_1\left(e_4 + \frac{1}{\tau}\right) - c_0 = 0.$$

Thus, if (4.13) is satisfied, (4.12) becomes

(4.14)
$$\Phi_3^*(\phi, n^2, q) = \left(\frac{dn^2}{l^2} + \phi\right)(\phi^2 + e_1)(\phi + e_2).$$

Then the roots of (4.14) are $\phi_{1,2} = \pm\sqrt{e_1}i, \phi_3 = -\frac{dn^2}{l^2} < 0, \phi_4 = -e_2 < 0$.

We now derive the transversality condition. Note that $\Phi_3^*(\phi, d) = \Phi_3^*(\phi + \frac{dn^2}{l^2})$. If $d = 0$, let ϕ^* be a root of $\Phi_3^*(\phi) = 0$. Then $\Phi_3^*(\phi + \frac{dn^2}{l^2}) = 0$ if $\phi + \frac{dn^2}{l^2} = \phi^*$; that actually is $\phi = \phi^* - \frac{dn^2}{l^2}$. This means that $Re(\phi) = Re(\phi^*) - \frac{dn^2}{l^2}$. So $\frac{dRe(\phi)}{dd} = -\frac{n^2}{l^2} < 0$ for $n = 1, 2 \ldots$ □

To make Theorem 4.4 clearer, we fixed the parameters as given in Table 1 and calculated the bifurcation values of the diffusion rate d_i, the corresponding period $\rho_i = \rho_1 = \cdots = \rho_n = 2\pi/\phi_i = 2\pi/\sqrt{e_1}_{n=1}$, and frequency $1/\rho_i$. These are shown in Table 2.

TABLE 2
Diffusion rate, period, and frequency of the Hopf bifurcation for $N_T = 2$.

Wave number i	Diffusion rate d_i	Period ρ_i	Frequency $1/\rho_i$
1	$0.032l^2$	8.0252	0.1246
2	$0.008l^2$	8.0252	0.1246
...	...	...	...
n	$\dfrac{0.032l^2}{n^2}$	8.0252	0.1246

Remark 4.5. As noted above, if ϕ^* is a root of the characteristic equation with $d = 0$, then $\phi^* - dn^2$, $n = 0, 1, \ldots$ are roots of (4.12). Thus the presence of diffusion is *stabilizing*, at least in terms of local stability of equilibrium points. This means that we can only expect diffusion-induced Hopf bifurcation of unstable equilibrium points. Nevertheless, in the next section we will show that the presence of diffusion can affect the behavior of the system.

5. Numerical simulations. In this section, we show numerical simulations using MATLAB [20] with the parameter values in Table 1 to illustrate the manifestation of Hopf bifurcations in the nonlinear model (4.1). The initial conditions used for the numerical simulations of (4.1) are primarily in the form

(5.1)
$$N(x,0) = N_0 + 0.1\cos(kx), \ P(x,0) = P_0, \ Z(x,0) = Z_0, \ Q(x,0) = Q_0, \quad k = 1, 3,$$

where N_0, P_0, Z_0, Q_0 are constants. Thus the total biomass in the system is $N_T = N_0 + P_0 + Z_0 + Q_0$, and the different choices for k allow us to study the effect of spatially inhomogenous perturbations on the solution. The numerical solutions are found using the finite difference method [27].

We first discuss the case with no diffusion, that is, the model (4.1) with $d = 0$, which was studied in [17]. Using the parameters in Table 1, the authors gave numerical evidence that the equilibrium point E_3^* loses stability via a Hopf for N_T sufficiently large. Using the program XPPAUT [6], we created a numerical bifurcation diagram for (4.1) using N_T as the bifurcation parameter; see Figure 3(a). This shows that the equilibrium point E_3^* undergoes a supercritical Hopf bifurcation at $N_T = N_{TH} \approx 1.2$.

Based on the analysis in the previous section, we expect that if $N_T < N_{TH}$ the equilibrium point E_3^* will be stable and no diffusion-induced Hopf bifurcation is possible. Numerical simulations of the model (4.1) with $N_T = 0.9$ and $N_T = 1.1$ confirm this, although for N_T near N_{TH} there can be long oscillatory transients; see Figure 4. Also, the smaller the value of d, the longer the effect of the inhomogeneous perturbation persists.

For $N_T > N_{TH}$ we expect that a spatially homogenous periodic solution will always exist, corresponding to the periodic solution of the ODE system. Numerical
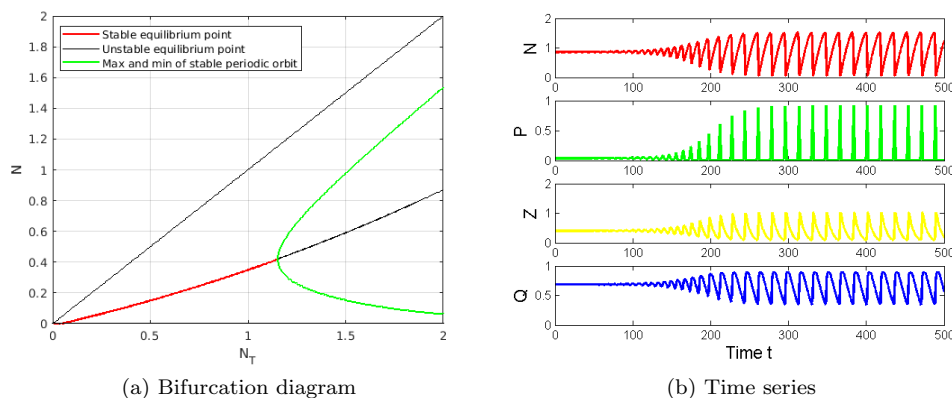

(a) Bifurcation diagram (b) Time series

FIG. 3. (a) *Bifurcation diagram for the ODE model of* [17], *which corresponds to* (4.1) *with* $d = 0$. (b) *Numerical simulation showing stable periodic orbit corresponding to* $N_T = 2$. *Parameter values are as in Table* 1.

(a) $\cos(x)$, $d = 0.002$ (b) $\cos(3x)$, $d = 0.002$

(c) $\cos(x)$, $d = 0.0036$ (d) $\cos(3x)$, $d = 0.0036$

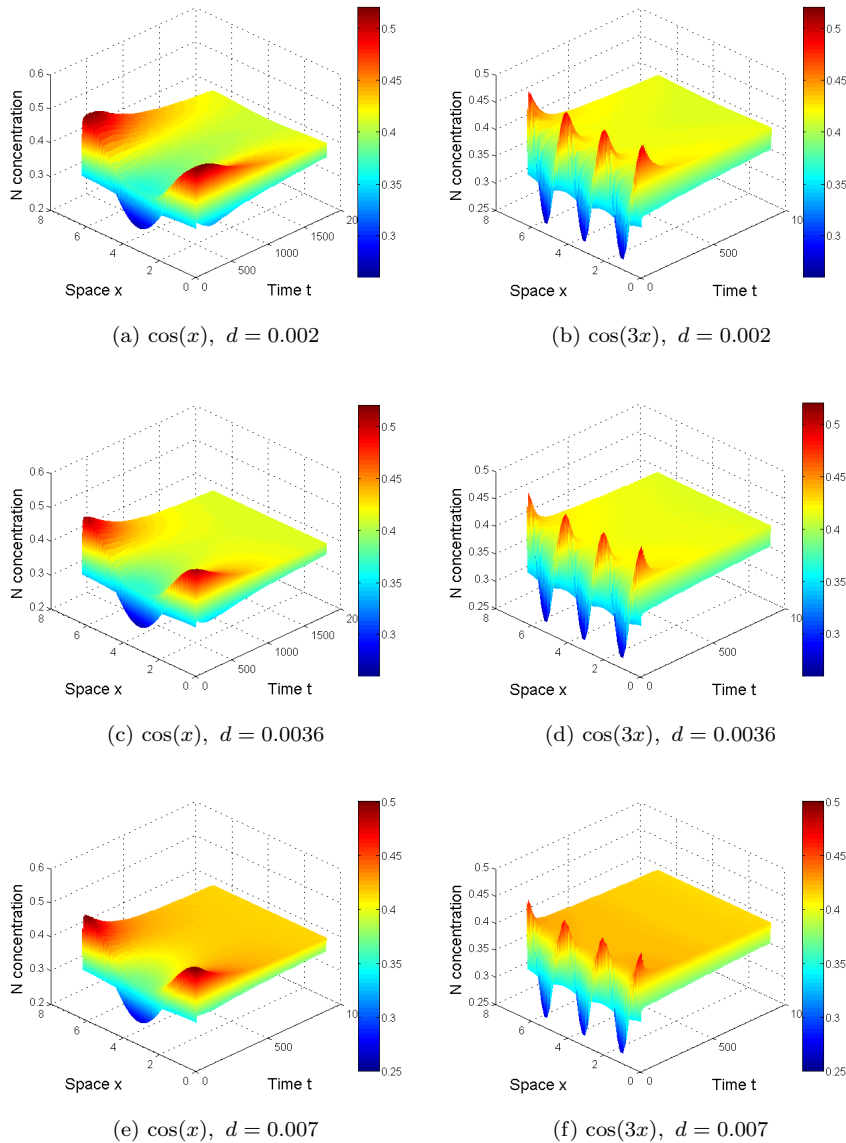(e) $\cos(x)$, $d = 0.007$ (f) $\cos(3x)$, $d = 0.007$

FIG. 4. *Solutions under different perturbations with $N_T = 1.1$. The initial values are given by* (5.1) *with $N_0 = 0.366855$, $P_0 = 0.0359$, $Z_0 = 0.2093$, $Q_0 = 0.4879$, and perturbation as shown.*

simulations with spatially homogenous initial conditions confirm this (not shown). Further, diffusion-induced Hopf bifurcation of the unstable equilibrium point E_3^* is possible; the bifurcation values are given in Table 2. Note that, as d decreases through each critical Hopf value, the real part of a pair of complex conjugate eigenvalues of E_3^* increases. Thus for $d > d_1$ there is one pair with positive real part, for $d_2 < d < d_1$ there are two pairs, and so on. We explore the implications of this in the rest of this section.

Figure 5 shows bistability for $N_T = 2$. When $d = 0.007$, there exists an inhomogenous solution with regular oscillations both on the time t and space x in Figure 5(f), while for the case with $k = 3$ in the initial displacement of the nutrients, the
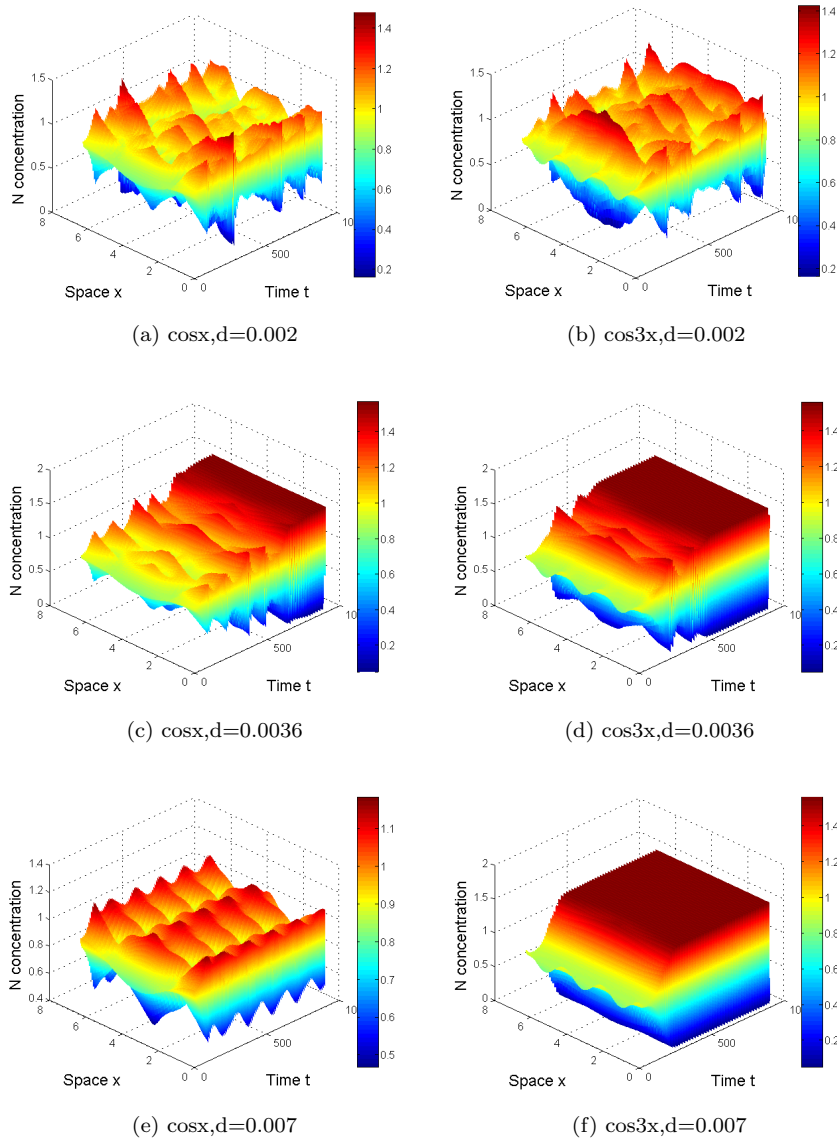
(a) cosx,d=0.002   (b) cos3x,d=0.002

(c) cosx,d=0.0036   (d) cos3x,d=0.0036

(e) cosx,d=0.007   (f) cos3x,d=0.007

FIG. 5. *Bistability under different perturbations for* $N_T = 2$. *The initial values are* $N_0 = 0.866855 + 0.1 \cos x \ (\cos 3x)$, $P_0 = 0.0359$, $Z_0 = 0.4093$, *and* $Q_0 = 0.6879$.

solution is homogeneous (Figure 5(g)). When the value of d is decreased to 0.0036, we can see a transient in the $k = 1$ initial condition; the solution changes from the inhomogeneous to homogeneous (Figure 5(c)), while for the $k = 3$ case, the inhomogeneity disappears more quickly (Figure 5(d)). As the d decreases to 0.002, the solutions are all significantly perturbed (Figure 5(a) and (b)). To make the above dynamics more clear, we present the contour plot of each solution at the end time from 700 to 900 in Figure 6.

Figure 7 shows the analysis of the spatial frequency and temporal frequency of the solutions with $d = 0.002, 0.0036$, and 0.007 in the logarithmic scale. These plots were obtained with the FFT function in MATLAB [20]. The first subplot shows that the
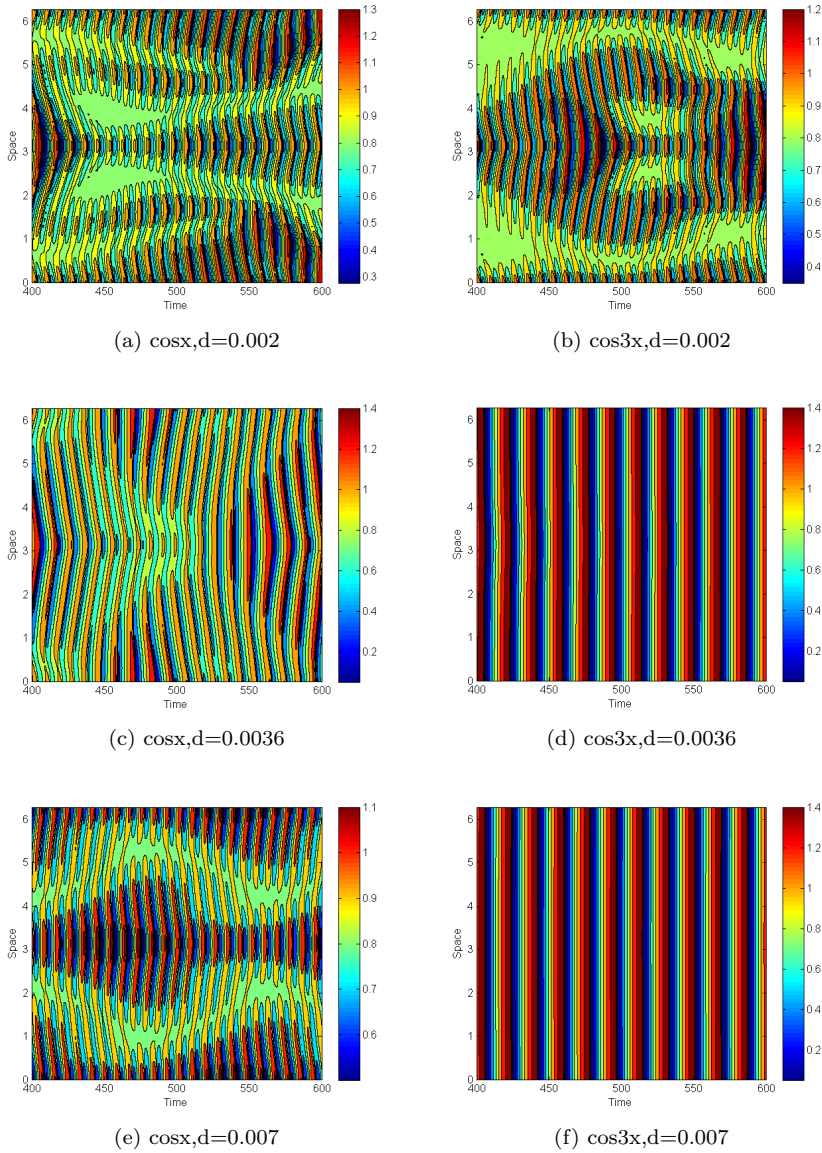
(a) cosx,d=0.002

(b) cos3x,d=0.002

(c) cosx,d=0.0036

(d) cos3x,d=0.0036

(e) cosx,d=0.007

(f) cos3x,d=0.007

FIG. 6. *The contour plot of* $N(x,t)$ *for* $x \in [700, 900]$. *The initial values are* $N_0 = 0.866855 + 0.1\cos x$ $(\cos 3x)$, $P_0 = 0.0359$, $Z_0 = 0.4093$, *and* $Q_0 = 0.6879$.

two cases with stronger diffusion have essentially the same power spectrum versus the spatial frequency, whereas the case with the weakest diffusion has much more power at the small length scales. This is not surprising since diffusion is known to dissipate the smaller length scales preferentially faster than the larger scales. In the second subplot, we see that the cases with $d = 0.02$ and $d = 0.07$ each have peaks in the power at the same temporal frequencies, but their profiles differ. The first frequency is what is predicted by the theory for spatially inhomogeneous Hopf bifurcation and its superharmonics. This is in contrast to the power for the case with $d = 0.0036$ that has the first peak at the frequency predicted of the theory for spatially homogeneous
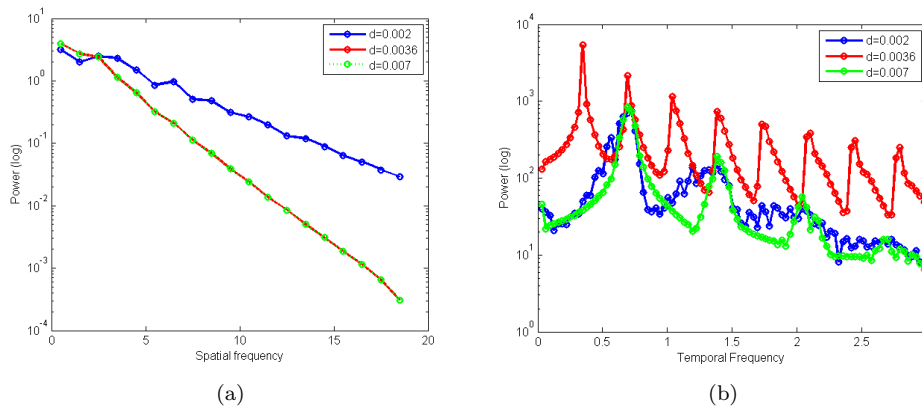
FIG. 7. (a) *Power vs spatial frequency,* (b) *Power vs temporal frequency for* $d = 0.002, 0.0036, d = 0.007$ *at the end time for* $t \in [700, 900]$. *The initial values are* $N_0 = 0.866855 + 0.1 \cos x (\cos 3x)$, $P_0 = 0.0359$, $Z_0 = 0.4093$, *and* $Q_0 = 0.6879$.

Hopf bifurcation. These observations are consistent our previous observation that the midstrength diffusion case tended to a homogeneous state but the others did not. We surmise that there is bistability in that the solutions can converge to ones that are spatially homogeneous or inhomogeneous, but we have not been able to ascertain why one appears in favor of the other in these simulations.

6. Discussion. We investigate the dynamics of a diffusion-reaction model with spatio-temporal delays to offer insights into the plankton communities by studying how the dynamics depend on the diffusion rates and the total biomass of the ecosystem.

Inspired by [9], we begin with proposing a new local stability theorem of a generalized three-dimensional system with diffusion and spatio-temporal delay. Our work extends that of [9] from two to three dimensions and incorporates the general spatial domain $(0, l\pi)$. We then study the local stability for the three types of equilibrium of the NPZ model (2.1). The local stability of the equilibrium solutions depends on the total biomass of the system, the mean delay, and the zooplankton grazing function form of $h(P)$. By comparing the conditions of the ODEs and those of the PDEs, we find that the diffusion has no impact on deducing the local instability of all three equilibrium solutions. Further, from calculation of the Hopf bifurcation value, all the real parts of eigenvalues when the diffusion constant satisfies $d \neq 0$ are less than the corresponding one when $d = 0$. Also from the simulations we explored, solutions are relatively ordered with a larger value of d. Both calculations and simulations show that the presence of diffusion has a stabilizing effect.

While the ecosystem is more stable under the effect of diffusion, it does have some complex dynamics. We verify that when a sufficient quantity of nutrients is provided, the plankton communities could experience different types of bistability, including homogeneous and inhomogeneous solutions, persistent and transient oscillations, which depend on the value of the diffusion constant d.

We note that throughout our analysis the diffusion constant always appears in the ratio d/l^2. This means that changing the size of the spatial domain has an equivalent effect to changing the diffusion constant. Thus, for example, raising the level of a lake due to either natural or artificial causes can have a destabilizing effect on the ecosystem.

There are many ways that our model could be extended. We have focused on diffusion dominated by the movement of the water, leading to equal diffusion constants for all the species. In future work, it will be of interest to explore the impact of different diffusion rates for each species. Further factors could be added to the model by considering different size structures, biodiversity, and sinking rates of plankton, as in [2, 4, 5, 15, 18, 22, 30]. It may be more realistic for the variables to have species diversity, the parameters to have size-dependence and/or age-dependence, and the ecosystem to have sinking rates. Thus, it would be intriguing to see how diffusion affects such ecosystems.

7. Appendix: Proof of Lemma 3.1.

Proof. By a well known result in complex variable theory [23], when $\Phi(\phi, n^2, q) = 0$ has no roots on the imaginary axis, the number of roots of this equation in the right half complex plane is

$$\lim_{R \to \infty} \frac{1}{2\pi i} \int_{C(R)} \frac{\Phi'(\phi, n^2, q)}{\Phi(\phi, n^2, q)} \mathrm{d}\phi.$$

Here, prime denotes differentiation with respect to ϕ, and $C(R)$ is the contour $C(R_1) \bigcup C(R_2)$, traversed in the anticlockwise sense, where

$$C(R_1) = \{\phi = ik : k \in [-R, R]\}, \ C(R_2) = \left\{\phi = Re^{i\theta} : \theta \in \left[-\frac{1}{2}\pi, \frac{1}{2}\pi\right]\right\}.$$

This contour is completely contained in the right half plane $\mathrm{Re}\phi \geq 0$. And the number of roots of $\Phi(\phi, n^2, q)$ inside $C(R)$ is

$$\frac{1}{2\pi i} \int_{C(R)} \frac{\Phi'(\phi, n^2, q)}{\Phi(\phi, n^2, q)} \mathrm{d}\phi = \frac{1}{2\pi i} \left(\int_{C(R_1)} \frac{\Phi'(\phi, n^2, q)}{\Phi(\phi, n^2, q)} \mathrm{d}\phi + \int_{C(R_2)} \frac{\Phi'(\phi, n^2, q)}{\Phi(\phi, n^2, q)} \mathrm{d}\phi \right).$$

There are two steps to prove (3.8). The first step is to prove that

$$(7.1) \qquad \frac{1}{2\pi i} \int_{C(R_1)} \frac{\Phi'(\phi, n^2, q)}{\Phi(\phi, n^2, q)} \mathrm{d}\phi = -\frac{1}{\pi} arg\Phi(iR, n^2, q).$$

The second one is to prove that

$$(7.2) \qquad \lim_{R \to \infty} \frac{1}{2\pi i} \int_{C(R_2)} \frac{\Phi'(\phi, n^2, q)}{\Phi(\phi, n^2, q)} \mathrm{d}\phi = \frac{3}{2}.$$

For point ϕ on contour $C(R_1)$, the complex conjugate of $\bar{m}$ is

$$\overline{\bar{m}(ik + dn^2)} = \int_0^\infty e^{-ikt} e^{dn^2 t} m_i(t) \mathrm{d}t = \bar{m}(-ik + dn^2).$$

Thus, we have

$$(7.3) \qquad \overline{B_j(ik, n^2, q)} = B_j(-ik, n^2, q), \qquad j = 0, 1, 2.$$

It follows from (7.3) that we get

$$\overline{\Phi(ik, n^2, q)} = k^3 i - B_2(ik, n^2, q)k^2 - B_1(ik, n^2, q)ki + B_0(ik, n^2, q) = \Phi(-ik, n^2, q).$$

That is, $\overline{\Phi(\phi, n^2, q)} = \Phi(\bar{\phi}, n^2, q)$ for any $\phi \in C(R_1)$. From these, we can obtain that the roots of $\Phi(\phi, n^2, q) = 0$ occur in complex conjugate pairs. We have, inside $C(R_1)$,

$$\rho e^{iarg(\Phi(-iR))} = \Phi(-iR) = \overline{\Phi(iR)} = \overline{\rho e^{iarg(\Phi(iR))}} = \rho e^{-iarg(\Phi(iR))},$$

where ρ is the module of Φ. Thus, $iarg(\Phi(-iR)) = -iarg(\Phi(iR))$. The contour $C(R_1)$ is traced from $\phi = iR$ to $\phi = -iR$. Then using the argument principle of complex number,

$$\frac{1}{2\pi i}\int_{C(R_1)}\frac{\Phi'(\phi,n^2,q)}{\Phi(\phi,n^2,q)}\mathrm{d}\phi = \frac{arg\Phi(-iR,n^2,q) - arg\Phi(iR,n^2,q)}{2\pi} = -\frac{1}{\pi}arg\Phi(iR,n^2,q).$$

This completes the proof of (7.1). Next, we prove (7.2).

For any point ϕ on the contour $C(R_2)$ we have

$$|\bar{m}(\phi + dn^2)| \leq \int_0^\infty e^{-(\phi+dn^2)t}m(t)\mathrm{d}t \leq \int_0^\infty m(t)\mathrm{d}t = 1.$$

Also, we have

$$\left|\frac{\mathrm{d}\bar{m}(\phi + dn^2)}{\mathrm{d}\phi}\right| \leq \int_0^\infty te^{-(\phi+dn^2)t}m(t)\mathrm{d}t \leq \int_0^\infty tm(t)\mathrm{d}t = T_m.$$

Consequently, $B_j(\phi,n^2,q)$ are bounded functions of ϕ for $\mathrm{Re}\phi \geq 0$, with bounds K_j, and

$$B_j'(\phi,n^2,q) \leq Q_j(n^2,q)T_f \triangleq K_j', \quad j = 0,1,2,$$

where $Q_j(q)$ are the parameter polynomials. Note that

$$\frac{1}{2\pi i}\int_{C(R_2)}\frac{2}{\phi}\mathrm{d}\phi = \frac{1}{2\pi i}\int_{-\frac{\pi}{2}}^{\frac{\pi}{2}}\frac{2}{Re^{i\theta}}iRe^{i\theta}\mathrm{d}\theta = 1.$$

Then

$$\frac{1}{2\pi i}\int_{C(R_2)}\frac{\Phi'(\phi,n^2,q)}{\Phi(\phi,n^2,q)}\mathrm{d}\phi - \frac{3}{2} = \frac{1}{2\pi i}\int_{C(R_2)}\left(\frac{\Phi'(\phi,n^2,q)}{\Phi(\phi,n^2,q)} - \frac{3}{\phi}\right)\mathrm{d}\phi,$$

$$= \frac{1}{2\pi i}\int_{C(R_2)}\left(\frac{-B_2\phi - 2B_1 + B_1'\phi + B_0'}{\Phi} - \frac{3B_0}{\phi\Phi}\right)\mathrm{d}\phi,$$

where we abbreviate $B_j(\phi,n^2,q)$ and $B_j'(\phi,n^2,q)$ to B_j and B_j'. It follows from the bounds of B_j and B_j' that we have $|\Phi(iR,n^2,q)| \geq R^3 - K_2R^2 - K_1R - K_0$. Then we have

$$\lim_{R\to\infty}\frac{1}{2\pi i}\int_{C(R_2)}\left|\frac{\Phi'(\phi,n^2,q)}{\Phi(\phi,n^2,q)}\mathrm{d}\phi - \frac{3}{2}\right|$$

$$= \lim_{R\to\infty}\frac{1}{2\pi i}\int_{-\frac{\pi}{2}}^{\frac{\pi}{2}}\left|\left(\frac{-B_2Re^{i\theta} - 2B_1 + B_1'Re^{i\theta} + B_0'}{\Phi} - \frac{3B_0}{Re^{i\theta}\Phi}\right)Re^{i\theta}\right|\mathrm{d}\theta,$$

$$\leq \lim_{R\to\infty}\frac{1}{2\pi i}\int_{-\frac{\pi}{2}}^{\frac{\pi}{2}}\left|\left(\frac{B_2Re^{i\theta} + 2B_1 + B_1'Re^{i\theta} + B_0'}{\Phi} + \frac{3B_0}{Re^{i\theta}\Phi}\right)Re^{i\theta}\right|\mathrm{d}\theta,$$

$$\leq \lim_{R\to\infty}\frac{K_2R^2 + 2K_1R + K_1'R^2 + K_0'R + 3K_0}{2\pi(R^3 - K_2R^2 - K_1R - K_0)}\int_{-\frac{\pi}{2}}^{\frac{\pi}{2}}\mathrm{d}\theta$$

$$= \lim_{R\to\infty}\frac{K_2R^2 + 2K_1R + K_1'R^2 + K_0'R + 3K_0}{2(R^3 - K_2R^2 - K_1R - K_0)} = 0. \qquad \square$$

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