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STABILITY AND ASYMPTOTIC PROFILE OF STEADY STATE SOLUTIONS TO A REACTION-DIFFUSION PELAGIC-BENTHIC ALGAE GROWTH MODEL

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Abstract. By using bifurcation theory, we investigate the local asymptotical stability of non-negative steady states for a coupled dynamic system of ordinary differential equations and partial differential equations. The system models the interaction of pelagic algae, benthic algae and one essential nutrient in an oligotrophic shallow aquatic ecosystem with ample supply of light. The asymptotic profile of positive steady states when the diffusion coefficients are sufficiently small or large are also obtained.

1. **Introduction.** In this paper, we consider the following coupled system of two ordinary differential equations and two parabolic partial differential equations:

$$\begin{cases} \dfrac{\partial U}{\partial t} = D_u \dfrac{\partial^2 U}{\partial z^2} - s\dfrac{\partial U}{\partial z} + \dfrac{r_u RU}{R+\gamma_u} - m_u U, & 0<z<L_1, \quad t>0, \\ \dfrac{dV}{dt} = \dfrac{r_v WV}{W+\gamma_v} - m_v V, & t>0, \\ \dfrac{\partial R}{\partial t} = D_r \dfrac{\partial^2 R}{\partial z^2} + c_u\beta_u m_u U - \dfrac{c_u r_u RU}{R+\gamma_u}, & 0<z<L_1, \quad t>0, \\ \dfrac{dW}{dt} = \dfrac{b}{L_2}(W_{sed}-W) - \dfrac{a}{L_2}(W - R(L_1,t)) + c_v\beta_v m_v V - \dfrac{c_v r_v WV}{W+\gamma_v}, & t>0, \\ D_u\dfrac{\partial U}{\partial z}(0,t) - sU(0,t) = 0,\ D_u\dfrac{\partial U}{\partial z}(L_1,t) - sU(L_1,t) = 0, & t>0, \\ \dfrac{\partial R}{\partial z}(0,t) = 0, D_r\dfrac{\partial R}{\partial z}(L_1,t) = a(W(t) - R(L_1,t)), & t>0, \end{cases} \tag{1}$$

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which was proposed and analyzed in [33]. Here all the variables and parameters of the model (1) and their biological significance are listed in Table 1, and we assume that $s \in \mathbb{R}, \beta_u, \beta_v \in [0,1]$ and the remaining parameters are all positive constants. Model (1) characterizes the interactions of pelagic algae, benthic algae and one essential nutrient in an oligotrophic shallow aquatic ecosystem with ample supply of light (see Fig.1 of [33]). In view of practical biological facts in model (1), we have three basic assumptions: (i) $L_2 \ll L_1$; (ii) the benthic habitat closely contacts with the sediment and dissolved nutrients in the benthic habitat are well mixed and homogeneous in space; (iii) benthic algae move very slowly or are motionless, so they are spatially uniformly distributed.

TABLE 1. Variables and parameters of model (1) with biological meanings.

Symbol	**Meaning**	**Symbol**	**Meaning**
t	Time	z	Depth
U	Biomass density of pelagic algae	V	Biomass density of benthic algae
R	Concentration of dissolved nutrients in the pelagic habitat	W	Concentration of dissolved nutrients in the benthic habitat
D_u	Vertical turbulent diffusivity of pelagic algae	D_r	Vertical turbulent diffusivity of dissolved nutrients in the pelagic habitat
s	Sinking or buoyant velocity of pelagic algae	r_u, r_v	Maximum specific production rate of pelagic algae and benthic algae, respectively
m_u, m_v	Loss rate of pelagic and benthic algae, respectively	γ_u, γ_v	Half saturation constant for nutrient-limited production of pelagic algae and benthic algae, respectively
c_u, c_v	Phosphorus to carbon quota of pelagic algae and benthic algae, respectively	W_{sed}	Concentration of dissolved nutrients in the sediment
L_1	Depth of the pelagic habitat (below water surface)	L_2	Vertical extent of the benthic habitat
a	Nutrient exchange rate between pelagic and benthic habitat	b	Nutrient exchange rate between sediment and benthic habitat
β_u	Nutrient recycling proportion from loss of pelagic algal biomass	β_v	Nutrient recycling proportion from loss of benthic algal biomass

There is accumulating evidence suggesting that the distributions of pelagic algae in aquatic ecosystems exhibit strong spatial heterogeneity [3, 4, 12, 13, 15, 30]. In [33], the model (1) is established to consider the effect of spatial heterogeneity on the interactions of pelagic algae, benthic algae and one essential nutrient. The existence, uniqueness and classification of non-negative steady states are obtained in [33] to characterize sharp threshold conditions for the regime shift from extinction to coexistence of pelagic and benthic algaes.

The present paper is a continuation of studies in [33], and here we provide the answer to the following two questions:

1. the local asymptotic stability of non-negative steady states in model (1) by applying bifurcation theory and associated linear stability theory;
2. the asymptotic profile of positive steady states when the diffusion coefficients D_u, D_r are sufficiently small or large in model (1).

It has long been recognized that pelagic algae and benthic algae are both potentially important primary producers in the aquatic ecosystem. As a good indicator of water quality and climate change, pelagic algae generally drift in the water column of lakes and oceans ecosystem, and compete with each other for essential resources such as nutrition and light [3, 4, 12, 30, 31, 32]. It should be noted that the types of pelagic algae competing major resources are not the same in different aquatic environments. In an eutrophic aquatic environment, pelagic algae tend to compete only for light [5, 6, 7, 9, 11, 16, 18, 21], while in a shallow or oligotrophic aquatic environments, pelagic algae tend to compete only for nutrients [10, 19, 20, 26]. In the streams, rivers or shallow lakes, benthic algae provide the main energy base in driving production for higher trophic levels. Accordingly, benthic algae are often more important than pelagic algae in these situations. Especially, in some shallow and clear-water aquatic environments, both planktonic algae and benthic algae exist simultaneously and compete fiercely for nutrition and light [8, 14, 22, 24, 25]. This competitive relationship as one of the challenges associated with understanding benthic-pelagic coupling has been described by using ordinary differential equations [14, 22, 24, 25].

The rest of the paper is organized as follows. In Section 2, we introduce some basic preliminary results on bifurcation analysis in order to establish the local asymptotic stability of non-negative steady states in model (1). Section 3 is devoted to establishing the locally asymptotically stable results of non-negative steady states in model (1) by applying the bifurcation theorems. In Section 4, we investigate the asymptotic profile of positive steady states when the diffusion coefficients are sufficiently small or large in model (1).

2. **Preliminaries.**

In this section, we give a short overview on some notations, definitions and well-known results for bifurcation theory that are important for the present study.

Let $(X, \|\cdot\|), (Y, \|\cdot\|)$ be Banach spaces and X is continuously embedding in Y. For a linear operator L, we denote $\mathcal{N}(L)$ as the null space of L and $\mathcal{R}(L)$ as the range space of L. Also $L[w]$ denotes the image of w under L, and if L is a multilinear operator, $L[w_1, w_2, \cdots, w_k]$ denote the image of $(w_1, w_2, \cdots, w_k)$ under L.

Consider a steady state equation

$$F(\lambda, u) = 0,$$

where $F : \mathbb{R} \times X \to Y$ is a nonlinear mapping and sufficiently smooth. For a given $(\lambda_0, u_0) \in \mathbb{R} \times X$, let U be a neighborhood of (λ_0, u_0) in $\mathbb{R} \times X$. The following bifurcation theorems are well-known, and we recall them for the convenience of readers. The first result is the local bifurcation theory known as "bifurcation from simple eigenvalue", and the second result shows the stability of bifurcating solutions obtained in the first one.

Theorem 2.1 (Theorem 1.7 in [1]). *Assume that*

(a_1) $F(\lambda, u_0) = 0$ *for all* $(\lambda, u_0) \in U$*;*
(a_2) $\dim \mathcal{N}(F_u(\lambda_0, u_0)) = \operatorname{codim} \mathcal{R}(F_u(\lambda_0, u_0)) = 1$ *and* $\mathcal{N}(F_u(\lambda_0, u_0)) = \operatorname{span}\{w_0\}$*;*
(a_3) $F_{\lambda u}(\lambda_0, u_0)[w_0] \notin \mathcal{R}(F_u(\lambda_0, u_0))$.

Then the solution set of $F(\lambda, u) = 0$ *near* (λ_0, u_0) *consists precisely of the curves* $u = u_0$ *and* $\Gamma : \{(\lambda(s), u(s)) : s \in I := (-\varepsilon, \varepsilon)\}$*. Here* $\lambda : I \to \mathbb{R}, z : I \to Z$ *are both continuously differentiable functions such that* $u(s) = u_0 + sw_0 + sz(s), \lambda(0) = \lambda_0, z(0) = 0,$ *and*

$$\lambda'(0) = -\frac{\langle l, F_{uu}(\lambda_0, u_0)[w_0, w_0]\rangle}{2\langle l, F_{\lambda u}(\lambda_0, u_0)[w_0]\rangle},$$

where $l \in Y^*$ *(dual space of* Y*) satisfies* $\mathcal{R}(F_u(\lambda_0, u_0)) = \{\phi \in Y : \langle l, \phi\rangle = 0\}$ *and* Z *is the complement of* $\operatorname{span}\{w_0\}$ *in* X*.*

Theorem 2.2 (Corollary 1.13 and Theorem 1.16 in [2]). *If (a_1)-(a_3) hold and $\{(\lambda(t), u(t))\}$ is the corresponding solution curve Γ in Theorem 2.1, then there exist C^2 functions*

$$\gamma : (\lambda_0 - \varepsilon, \lambda_0 + \varepsilon) \to \mathbb{R}, z : (\lambda_0 - \varepsilon, \lambda_0 + \varepsilon) \to X, \mu : (-\delta, \delta) \to \mathbb{R}, w : (-\delta, \delta) \to X$$

such that

$$F_u(\lambda, u_0)z(\lambda) = \gamma(\lambda)z(\lambda) \text{ for } \lambda \in (\lambda_0 - \varepsilon, \lambda_0 + \varepsilon),$$
$$F_u(\lambda(\tau), u(\tau))w(\tau) = \mu(\tau)w(\tau) \text{ for } \tau \in (-\delta, \delta),$$

where $\gamma(\lambda_0) = \mu(0) = 0,\ z(\lambda_0) = w(0) = w_0$. Moreover, near $\tau = 0$ the functions $\mu(\tau)$ and $-\tau\lambda'(\tau)\gamma'(\lambda_0)$ have the same zeros and, when $\mu(\tau) \neq 0$, the same sign, or more precisely,

$$\lim_{\tau \to 0} \frac{-\tau\lambda'(\tau)\gamma'(\lambda_0)}{\mu(\tau)} = 1.$$

Next we recall the following global bifurcation results under essentially same conditions as the above local bifurcation theorem, and more results of its application can be found in [28, 29].

Theorem 2.3 (Theorem 4.3 in [23]). *If (a_1)-(a_3) hold and $F_u(\lambda, u)$ is a Fredholm operator for all $(\lambda, u) \in U$, then the curve Γ is contained in $\mathcal{C}$, which is a connected component of $\bar{S}$ where $S = \{(\lambda, u) \in U : F(\lambda, u) = 0, u \neq u_0\}$; and either $\mathcal{C}$ is not compact in U, or $\mathcal{C}$ contains a point (λ_*, u_0) with $\lambda_* \neq \lambda_0$.*

Let Γ be defined as in Theorem 2.1 and $\mathcal{C}$ be defined as in Theorem 2.3. We define $\Gamma_+ = \{(\lambda(s), u(s)) : s \in (0, \varepsilon)\}$, $\Gamma_- = \{(\lambda(s), u(s)) : s \in (-\varepsilon, 0)\}$ and $\mathcal{C}^+$ (resp. $\mathcal{C}^-$) as the connected component of $\mathcal{C} \setminus \Gamma_-$ which contains Γ_+ (resp. the connected component of $\mathcal{C} \setminus \Gamma_+$ which contains Γ_-).

Theorem 2.4 (Theorem 4.4 in [23]). *Assume that all conditions in Theorem 2.3 hold. If*

- (b_1) *$F_u(\lambda, u_0)$ is continuously differentiable in λ for $(\lambda, u_0) \in U$;*
- (b_2) *the norm function $u \mapsto \|u\|$ in X is continuously differentiable for any $u \neq 0$;*
- (b_3) *for $k \in (0, 1)$, $(1 - k)F_u(\lambda, u_0) + kF_u(\lambda, u)$ is a Fredholm operator if (λ, u_0) and (λ, u) are both in U.*

Then each of the sets $\mathcal{C}^+$ and $\mathcal{C}^-$ satisfies one of the following: (i) *it is not compact;* (ii) *it contains a point (λ_*, u_0) with $\lambda_* \neq \lambda_0$; or* (iii) *it contains a point $(\lambda, u_0 + z)$, where $z \neq 0$ and $z \in Z$.*

3. Bifurcation analysis for the algae growth model.

In this section, we investigate the local asymptotical stability of the non-negative steady state solutions of model (1) by using bifurcation method.

We first recall the following possible non-negative steady state solutions of model (1). Let $E_1 = (0, 0, R_1, W_1)$ be the nutrient-only semi-trivial steady state, where (R_1, W_1) solves

$$\begin{cases} R'' = 0,\ 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) = 0, \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)). \end{cases} \tag{2}$$

In fact, by (2), we have $E_1 = (0, 0, W_{sed}, W_{sed})$. Let $E_2 = (0, V_2, R_2, W_2)$ be the benthic algae-nutrient semi-trivial steady state, where (V_2, R_2, W_2) satisfies

$$\begin{cases} \dfrac{r_v W}{W+\gamma_v} - m_v = 0, \\ R'' = 0,\ 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) + c_v L_2 \left(\beta_v m_v - \dfrac{r_v W}{W+\gamma_v}\right) V = 0, \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)). \end{cases} \tag{3}$$

By solving (3), we find $V_2 = b(W_{sed} - W_2)/[c_v m_v L_2(1-\beta_v)]$, $R_2 = W_2 = \gamma_v m_v/(r_v - m_v)$. Let $E_3 = (U_3, 0, R_3, W_3)$ be the pelagic algae-nutrient semi-trivial steady state, where (U_3, R_3, W_3) solves

$$\begin{cases} D_u U'' - sU' + \left(\dfrac{r_u R}{R+\gamma_u} - m_u\right) U = 0, & 0 < z < L_1, \\ D_r R'' + c_u \beta_u m_u U - \dfrac{c_u r_u R U}{R+\gamma_u} = 0, & 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) = 0, \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)). \end{cases} \tag{4}$$

From (4), we obtain $W_3 = (aR_3(L_1) + bW_{sed})/(a+b)$. Let $E_4 = (U_4, V_4, R_4, W_4)$ be a coexistence steady state, where (U_4, V_4, R_4, W_4) satisfies

$$\begin{cases} D_u U'' - sU' + \left(\dfrac{r_u R}{R+\gamma_u} - m_u\right) U = 0, & 0 < z < L_1, \\ \dfrac{r_v W}{W+\gamma_v} - m_v = 0, \\ D_r R'' + c_u \beta_u m_u U - \dfrac{c_u r_u R U}{R+\gamma_u} = 0, & 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) + c_v L_2 \left(\beta_v m_v - \dfrac{r_v W}{W+\gamma_v}\right) V = 0, \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)). \end{cases} \tag{5}$$

Proposition 3.1 in [33] shows that a coexistence steady state can only exist when $0 < m_u \le r_u$ and $0 < m_v \le r_v$. By solving (5), we have

$$V_4 = \frac{b(W_{sed} - W_4) - a(W_4 - R_4(L_1))}{c_v m_v L_2(1-\beta_v)},\ W_4 = \frac{\gamma_v m_v}{r_v - m_v}. \tag{6}$$

From Lemma 3.10 in [33], we have $0 < R_4(L_1) < \gamma_v m_v/(r_v - m_v)$. This means that if

$$0 \le \beta_v < 1, \quad 0 < m_v < \frac{r_v b W_{sed}}{\gamma_v(a+b) + bW_{sed}},$$

then $V_4, W_4 > 0$.

The local asymptotically stability results of E_1 and E_2 have been established in [33] (see Theorems 3.2 and 3.4). The existence of E_3 and E_4 were proved in [33] by using a priori estimates and degree theory, and it is also known that each of E_3 and E_4 is unique and non-degenerate (see Theorems 3.8 and 3.11 in [33]). We now are concerned with the local asymptotical stability of E_3 and E_4 with the help of bifurcation analysis. In the following discussion, taking m_u as the bifurcation parameter, we explore the following two cases:

- E_3 bifurcates from E_1 at $m_u = m_u^*$, where $m_u^* = r_u W_{sed}/(W_{sed} + \gamma_u)$;
- E_4 bifurcates from E_2 at $m_u = m_u^{**}$, where $m_u^{**} = r_u \gamma_v m_v / [\gamma_v m_v + \gamma_u (r_v - m_v)]$.

3.1. E_3 **bifurcating from** E_1 **at** $m_u = m_u^*$. In this subsection, we consider the bifurcation of pelagic algae-nutrient semi-trivial steady state E_3 from nutrient-only semi-trivial steady state E_1 at $m_u = m_u^*$. We first investigate the local bifurcation theorem and local asymptotical stability of E_3. For the convenience of the following discussion, we denote

$$h = (\beta_u - 1) c_u m_u^*, \ c_1 = \left[\frac{D_u^2 h}{s^2 D_r} + \frac{D_u h(a+b)}{abs} \right] e^{\frac{sL_1}{D_u}} - \left[\frac{D_u h L_1}{s D_r} + \frac{D_u h (a+b)}{abs} \right], \tag{7}$$

$$\Phi(z) = e^{(s/D_u)z}, \ \Psi(z) = \frac{D_u h}{s D_r} z - \frac{D_u^2 h}{s^2 D_r} e^{(s/D_u)z} + c_1 \quad \text{for} \quad 0 < z < L_1, \tag{8}$$

and

$$\Theta = \frac{a}{a+b} \Psi(L_1). \tag{9}$$

Theorem 3.1. *If*

$$0 \le \beta_u < 1, \ \ 0 < m_u < m_u^*, \ \ m_v > 0, \tag{10}$$

then there is a smooth curve Γ_{E_3} of positive solutions of (4) bifurcating from the line of trivial solutions $\hat{\Gamma}_{E_1} = \{(m_u, 0, W_{sed}, W_{sed}) : m_u > 0\}$ at $m_u = m_u^*$. Moreover,

1. *near $\{(m_u^*, 0, W_{sed}, W_{sed})\}$, there exists a positive constant $\delta > 0$ such that all the positive solutions of (4) lie on a smooth curve*
$$\hat{\Gamma}_{E_3} = \{(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau)) : 0 < \tau < \delta\},$$
where $U(\tau, z) = \tau\Phi(z) + \tau g_1(\tau, z), R(\tau, z) = W_{sed} + \tau\Psi(z) + \tau g_2(\tau, z), W(\tau) = W_{sed} + \tau\Theta + \tau g_3(\tau)$, and $m_u(\tau), g_i(\tau, \cdot)(i = 1, 2)$, $g_3(\tau)$ are smooth functions defined for $\tau \in (0, \delta)$ such that $m_u(0) = m_u^*$, $m_u'(0) < 0$, $g_i(0, \cdot) = 0 (i = 1, 2)$ and $g_3(0) = 0$;
2. *for $\tau \in (0, \delta)$, the bifurcating solution $(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau))$ is locally asymptotically stable with respect to the following reduced equation without benthic algae:*
$$\begin{cases} \dfrac{\partial U}{\partial t} = D_u \dfrac{\partial^2 U}{\partial z^2} - s\dfrac{\partial U}{\partial z} + \dfrac{r_u R U}{R + \gamma_u} - m_u U, & 0 < z < L_1, \ t > 0, \\ \dfrac{\partial R}{\partial t} = D_r \dfrac{\partial^2 R}{\partial z^2} + c_u \beta_u m_u U - \dfrac{c_u r_u R U}{R + \gamma_u}, & 0 < z < L_1, \ t > 0, \\ \dfrac{dW}{dt} = \dfrac{b}{L_2}(W_{sed} - W) - \dfrac{a}{L_2}(W - R(L_1, t)), & t > 0, \\ D_u \dfrac{\partial U}{\partial z}(0, t) - sU(0, t) = 0, \ D_u \dfrac{\partial U}{\partial z}(L_1, t) - sU(L_1, t) = 0, & t > 0, \\ \dfrac{\partial R}{\partial z}(0, t) = 0, D_r \dfrac{\partial R}{\partial z}(L_1, t) = a(W(t) - R(L_1, t)), & t > 0. \end{cases} \tag{11}$$
3. *If in addition $m_v > r_v W_{sed}/(W_{sed} + \gamma_v)$, then the bifurcating steady state solution $E_3(\tau) = (m_u(\tau), U(\tau, z), 0, R(\tau, z), W(\tau))$ is locally asymptotically stable with respect to the full system (1) for $\tau \in (0, \delta)$.*

The result in part 2 here shows that the bifurcating pelagic-algae-only steady state solution E_3 is locally asymptotically stable in the absence of initial benthic algae (in such case, the system (1) is effectively reduced to (11). On the other hand, if initially there is benthic algae but the death rate of the benthic algae m_v is large, then part 3 shows that the bifurcating pelagic-algae-only steady state solution E_3 is locally asymptotically stable with respect to the full system. We prove part 1 and 2 of Theorem 3.1 here, and postpone the proof of part 3 to subsection 3.2.

Proof of Theorem 3.1 part 1 and 2. Let

$$X_1 := \{U \in C^2[0, L_1] : D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0\},$$
$$X_2 := \{R \in C^2[0, L_1] : R'(0) = 0\}, \quad Y := C[0, L_1].$$

Denote $\mathcal{X} := X_1 \times X_2 \times \mathbb{R}$, and define a nonlinear mapping $F : \mathbb{R}^+ \times \mathcal{X} \to Y \times Y \times \mathbb{R} \times \mathbb{R}$ by

$$F(m_u, U(z), R(z), W) = \begin{pmatrix} D_u U''(z) - sU'(z) + \dfrac{r_u R(z)U(z)}{R(z) + \gamma_u} - m_u U(z) \\ D_r R''(z) + c_u \beta_u m_u U(z) - c_u \dfrac{r_u R(z)}{R(z) + \gamma_u} U(z) \\ \dfrac{b}{L_2}(W_{sed} - W) - \dfrac{a}{L_2}(W - R(L_1)) \\ D_r R'(L_1) - a(W - R(L_1)) \end{pmatrix}. \tag{12}$$

It is clear that $F(m_u, 0, W_{sed}, W_{sed}) = 0$ which implies that the assumption (a_1) holds in Theorem 2.1.

We now prove that (a_2) holds in Theorem 2.1. It follows from Theorem 3.8 in [33] that (4) has a semi-trivial steady state E_3 under the assumption (10). We linearize the system (12) about a steady state $(\bar{U}(z), \bar{R}(z), \bar{W})$ and obtain

$$\begin{aligned} &F_{(U,R,W)}(m_u, \bar{U}(z), \bar{R}(z), \bar{W})[\varphi(z), \phi(z), \zeta] \\ &= \begin{pmatrix} D_u \varphi''(z) - s\varphi'(z) + \left(\dfrac{r_u \bar{R}(z)}{\bar{R}(z) + \gamma_u} - m_u\right)\varphi(z) + \dfrac{r_u \gamma_u \bar{U}(z)}{(\bar{R}(z) + \gamma_u)^2}\phi(z) \\ \left(c_u \beta_u m_u - \dfrac{c_u r_u \bar{R}(z)}{\bar{R}(z) + \gamma_u}\right)\varphi(z) + D_r \phi''(z) - \dfrac{c_u r_u \gamma_u \bar{U}(z)}{(\bar{R}(z) + \gamma_u)^2}\phi(z) \\ \dfrac{a}{L_2}\phi(L_1) - \dfrac{a+b}{L_2}\zeta \\ D_r \phi'(L_1) - a(\zeta - \phi(L_1)) \end{pmatrix}, \end{aligned} \tag{13}$$

and then, at $(m_u, \bar{U}(z), \bar{R}(z), \bar{W}) = (m_u^*, 0, W_{sed}, W_{sed})$, by simple calculations we get

$$\begin{aligned} &F_{(U,R,W)}\left(m_u^*, 0, W_{sed}, W_{sed}\right)[\varphi(z), \phi(z), \zeta] \\ &= \begin{pmatrix} D_u \varphi''(z) - s\varphi'(z) \\ c_u m_u^*(\beta_u - 1)\varphi(z) + D_r \phi''(z) \\ \dfrac{a}{L_2}\phi(L_1) - \dfrac{a+b}{L_2}\zeta \\ D_r \phi'(L_1) - a(\zeta - \phi(L_1)) \end{pmatrix}. \end{aligned} \tag{14}$$

Denote $L := F_{(U,R,W)}\left(m_u^*, 0, W_{sed}, W_{sed}\right)$. If $[\Phi(z), \Psi(z), \Theta] \in \mathcal{N}(L)$, then we have

$$D_u \Phi''(z) - s\Phi'(z) = 0, \quad D_u \Phi'(z) - s\Phi(z)|_{z=0,L_1} = 0, \tag{15}$$

$$c_u m_u^* (\beta_u - 1)\Phi(z) + D_r \Psi''(z) = 0, \tag{16}$$

$$\frac{a}{L_2}\Psi(L_1) - \frac{a+b}{L_2}\Theta = 0, \tag{17}$$

$$D_r \Psi'(L_1) - a(\Theta - \Psi(L_1)) = 0. \tag{18}$$

By (15), we get easily that $\Phi(z) = e^{(s/D_u)z}$. Substituting $\Phi(z)$ into (16), we obtain the expression of $\Psi(z)$ in (8). Combining the boundary condition $D_r\Psi'(L_1) + ab/(a+b)\Psi(L_1) = 0$, which follows from (17) and (18), we can uniquely identify the constant c_1 as (7). Substituting $\Psi(z)$ into (17), we have $\Theta = \frac{a}{a+b}\Psi(L_1)$. This shows that $\dim \mathcal{N}(L) = 1$ and $\mathcal{N}(L) = \mathrm{span}\{(\Phi(z), \Psi(z), \Theta)\}$.

We next consider the codimension of $\mathcal{R}(L)$. Suppose that $(f_1(z), f_2(z), f_3, f_4)^T \in \mathcal{R}(L)$, then there exists $[\varphi(z), \phi(z), \zeta] \in C^2[0, L_1] \times C^2[0, L_1] \times \mathbb{R}$ such that $L[\varphi(z), \phi(z), \zeta] = (f_1(z), f_2(z), f_3, f_4)^T$, that is

$$D_u \varphi''(z) - s\varphi'(z) = f_1(z), \quad D_u \varphi'(z) - s\varphi(z)|_{z=0,L_1} = 0, \tag{19}$$

$$\left(c_u \beta_u m_u - c_u m_u^*\right)\varphi(z) + D_r \phi''(z) = f_2(z), \tag{20}$$

$$\frac{a}{L_2}\phi(L_1) - \frac{a+b}{L_2}\zeta = f_3, \tag{21}$$

$$D_r \phi'(L_1) - a(\zeta - \phi(L_1)) = f_4. \tag{22}$$

Multiplying both sides of (15) and (19) by $\varphi(z)$ and $\Phi(z)$, respectively, subtracting and integrating on $[0, L_1]$, also combining the boundary conditions in (15) and (19), we have

$$\begin{aligned} \frac{1}{D_u}\int_0^{L_1} f_1(z)dz &= \int_0^{L_1} \left[\Phi(z)\left(\varphi'(z)e^{-\frac{sz}{D_u}}\right)' - \varphi(z)\left(\Phi'(z)e^{-\frac{sz}{D_u}}\right)'\right]dz \\ &= \left[\Phi(z)\varphi'(z) - \varphi(z)\Phi'(z)\right]\Big|_0^{L_1} \\ &\quad - \int_0^{L_1}\left(\varphi'(z)e^{-\frac{sz}{D_u}}\Phi'(z) - \Phi'(z)e^{-\frac{sz}{D_u}}\varphi'(z)\right)dz \\ &= 0. \end{aligned}$$

This shows that

$$\mathcal{R}(L) = \left\{(f_1(z), f_2(z), f_3, f_4)^T \in Y \times Y \times \mathbb{R} \times \mathbb{R} : \int_0^{L_1} f_1(z)dz = 0\right\},$$

and $\mathrm{codim}\mathcal{R}(L) = 1$.

From (13), we have

$$F_{m_u(U,R,W)}\left(m_u^*, 0, W_{sed}, W_{sed}\right)[\Phi(z), \Psi(z), \Theta] = \left(-\Phi(z) \quad c_u\beta_u\Phi(z) \quad 0 \quad 0\right)^\tau,$$

which yields that $F_{m_u(U,R,W)}\left(m_u^*, 0, W_{sed}, W_{sed}\right)[\Phi(z), \Psi(z), \Theta] \notin \mathcal{R}(L)$. This implies that the assumption (a$_3$) holds in Theorem 2.1.

By applying Theorem 2.1, we conclude that there exists an open interval $I = (0, \delta)$ with $\delta > 0$ and C^1 functions $m_u : I \to \mathbb{R}$, $g_i(\cdot, z) : I \to Z (i = 1, 2)$, and $g_3 : I \to Z$, where Z is any complement of $\mathrm{span}\{(\Phi(z), \Psi(z), \Theta)\}$, such that the solution set of (4) near $(m_u^*, 0, W_{sed}, W_{sed})$ consists precisely of the curves

$$\hat{\Gamma}_{E_1} = \{(m_u, 0, W_{sed}, W_{sed}) : m_u > 0\},$$

and

$$\hat{\Gamma}_{E_3} = \{(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau)) : \tau \in I\},$$

where $U(\tau, z) = \tau\Phi(z) + g_1(\tau, z), R(\tau, z) = W_{sed} + \tau\Psi(z) + g_2(\tau, z), W(\tau) = W_{sed} + \tau\Theta + g_3(\tau), m_u(0) = m_u^*,\ g_i(0, \cdot) = 0 (i = 1, 2),\ g_3(0) = 0$ and

$$\begin{aligned} m_u'(0) &= -\frac{\left\langle l,\ F_{(U,R,W)(U,R,W)}\left(m_u^*, 0, W_{sed}, W_{sed}\right)[\Phi(z), \Psi(z), \Theta]^2\right\rangle}{2\left\langle l,\ F_{m_u(U,R,W)}\left(m_u^*, 0, W_{sed}, W_{sed}\right)[\Phi(z), \Psi(z), \Theta]\right\rangle} \\ &= -\frac{\displaystyle\int_0^{L_1} \frac{2r_u\gamma_u}{(W_{sed} + \gamma_u)^2}\Phi(z)\Psi(z)dz}{\displaystyle -2\int_0^{L_1} e^{\frac{sz}{D_u}}\, dz}, \end{aligned} \tag{23}$$

where l is a linear functional on $Y \times Y \times \mathbb{R} \times \mathbb{R}$ defined as $\langle l, (f_1(z), f_2(z), f_3, f_4)\rangle = \int_0^{L_1} f_1(z)dz$. From (10) and (7), we have $h < 0$, and from the fact that $\Psi(z)$ is nondecreasing in z (since $\Psi'(z) = \frac{D_u h}{sD_r}(1 - e^{\frac{sz}{D_u}})$), we have $\Psi(z) \leq \Psi(L_1) = \frac{D_u h(a+b)}{abs}(e^{\frac{sL_1}{D_u}} - 1) < 0$ on $[0, L_1]$. According to (23), we get $m_u'(0) < 0$. This completes the proof of part 1.

Now we consider the stability of bifurcating solutions. In view of Theorem 2.2, there exist continuously differentiable functions

$$\gamma : (m_u^* - \varepsilon, m_u^* + \varepsilon) \to \mathbb{R},\ [\hat{\varphi}, \hat{\phi}, \hat{\zeta}] : (m_u^* - \varepsilon, m_u^* + \varepsilon) \to \mathcal{X},\ \mu : (-\delta, \delta) \to \mathbb{R}$$

and $[\varphi^*, \phi^*, \zeta^*] : (-\delta, \delta) \to \mathcal{X}$ such that

$$\begin{aligned} &F_{(U,R,W)}\left(m_u, 0, W_{sed}, W_{sed}\right)[\hat{\varphi}(m_u), \hat{\phi}(m_u), \hat{\zeta}(m_u)] \\ =&\gamma(m_u)[\hat{\varphi}(m_u), \hat{\phi}(m_u), \hat{\zeta}(m_u), 0]^T, \end{aligned} \tag{24}$$

$$\begin{aligned} &F_{(U,R,W)}\left(m_u(\tau), U(\tau), R(\tau), W(\tau)\right)[\varphi^*(\tau), \phi^*(\tau), \zeta^*(\tau)] \\ =&\mu(\tau)[\varphi^*(\tau), \phi^*(\tau), \zeta^*(\tau), 0]^T. \end{aligned} \tag{25}$$

From (13), we have $\gamma(m_u) = m_u^* - m_u$, and $\gamma'(m_u) = -1$. Moreover $\gamma(m_u^*) = 0$ is the principal eigenvalue of $F_{(U,R,W)}\left(m_u, 0, W_{sed}, W_{sed}\right)$. Hence the perturbed eigenvalue $\mu(\tau)$ is also the principal eigenvalue of $F_{(U,R,W)}\left(m_u(\tau), U(\tau), R(\tau), W(\tau)\right)$. Now from Theorem 2.2 and $m_u'(0) < 0$, we find $\mu(\tau) < 0$ for $\tau > 0$ small. Hence $(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau))$ is locally asymptotically stable with respect to the system (11). This completes the proof of part 2. □

Remark 3.1. In Theorem 3.1, we assume that $0 \leq \beta_u < 1$. This is because that if $\beta_u = 1$, then (4) reduces to

$$\begin{cases} D_u U'' - sU' + \left(\dfrac{r_u R}{R + \gamma_u} - m_u\right)U = 0, & 0 < z < L_1, \\ D_r R'' + c_u m_u U - \dfrac{c_u r_u R U}{R + \gamma_u} = 0, & 0 < z < L_1, \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, & \\ R'(0) = R'(L_1) = 0. & \end{cases}$$

This means that pelagic algae and dissolved nutrients in the pelagic habitat constitute a closed system with internal continuous cycle in ecology. In this case, authors in [33] showed that $\lim\limits_{t\to\infty} \frac{1}{|\Omega|}\int_\Omega U(z, t)dz = \infty$ if $\beta_u = 1$ by numerical method. Considering practical biological significance, here we assume that $0 \leq \beta_u < 1$.

Next we prove the global bifurcation property of the branch $\hat{\Gamma}_{E_3}$. First we have the following *a priori* estimates for positive solutions (U_3, R_3, W_3) of (4).

Lemma 3.2. *Assume that $(U_3, R_3, W_3) \in C([0, L_1]) \times C([0, L_1]) \times \mathbb{R}_+$ is a positive solution of (4) and $\beta_u \in [0, 1)$. Then*

(i) $\frac{\beta_u \gamma_u m_u}{r_u - \beta_u m_u} \le R_3(z) < W_{sed}$ *for all* $z \in [0, L_1]$;

(ii) $0 < W_3 < W_{sed}$;

(iii) *for any $\varepsilon > 0$, there exists a positive constant $A(\varepsilon)$ such that $\|U_3\|_\infty \le A(\varepsilon)$ if $m_u \in [\varepsilon, m_u^*)$, and $\|U_3^{m_u}\|_\infty \to \infty$ as $m_u \to 0$.*

Proof. The results have been proved in Lemma 3.6 of [33] except the statement that $\|U_3^{m_u}\|_\infty \to \infty$ as $m_u \to 0$. Suppose this is not true, then there exists a sequence of m_u, denoted by $m_n := m_u^n$, and corresponding positive solutions (U_3^n, R_3^n, W_3^n) of (4) such that $m_n \to 0$ and $\|U_3^n\|_\infty \to C < \infty$ as $n \to \infty$. By using L^p theory for elliptic operators and the Sobolev embedding theorem, after passing to a subsequence if necessary, we may assume that $U_3^n \to U^*$ in $C^1[0, L_1]$ as $n \to \infty$ since $\{U_3^n\}$ is bounded in $L^\infty(0, L_1)$. Integrating the first equation of (4) on $[0, L_1]$, we have

$$\int_0^{L_1} \frac{r_u R_3^n(z)}{R_3^n(z) + \gamma_u} U_3^n(z) dz \to 0, \quad \text{as } m_n \to 0. \tag{26}$$

From part (i) and (26), we obtain that

$$\int_0^{L_1} U_3^n(z) dz \to 0, \quad \text{as } m_n \to 0. \tag{27}$$

On the other hand, integrating the second equation of (4) on $[0, L_1]$, we get

$$0 = D_r (R_3^n)'(L_1) + c_u \beta_u m_n \int_0^{L_1} U_3^n(z) dz - \int_0^{L_1} \frac{c_u r_u R_3^n(z)}{R_3^n(z) + \gamma_u} U_3^n(z) dz,$$

which contradicts with (26)–(27) and R_3^n is strictly increasing on $[0, L_1]$ showed in Lemma 3.6 of [33]. Therefore $\|U_3^{m_u}\|_\infty \to \infty$ as $m_u \to 0$. □

Now we state the global bifurcation theorem of the steady state solution E_3.

Theorem 3.3. *Let S^+ be the set of positive solutions to (4). Then S^+ is a smooth curve in $\mathbb{R}^+ \times \mathcal{X}$ in form*

$$S^+ = \{(m_u, U_3(m_u, z), R_3(m_u, z), W_3(m_u)) : 0 < m_u < m_u^*\} \tag{28}$$

satisfying $\lim_{m_u \to (m_u^*)^-} (U_3(m_u, \cdot), R_3(m_u, \cdot), W_3(m_u)) = (0, W_{sed}, W_{sed})$, *and* $\lim_{m_u \to 0^+} ||U_3(m_u, \cdot)||_\infty = \infty$.

Proof. From Theorem 3.3 and Remark 3.4 of [23], it is easy to check that for any fixed $(\tilde{U}(z), \tilde{R}(z), \tilde{W}) \in \mathcal{X}$,

$$F_{(U,R,W)}(m_u, \tilde{U}(z), \tilde{R}(z), \tilde{W}) : \mathcal{X} \to Y \times Y \times \mathbb{R} \times \mathbb{R}$$

is a Fredholm operator with index zero. By applying Theorem 2.3, we obtain a connected component $\mathcal{C}$ of the set S of all solutions to (4) emanating from $(m_u, U(z), R(z), W) = (m_u^*, 0, W_{sed}, W_{sed})$. Let

$$P = \Big\{(U(z), R(z), W) \in \mathcal{X} : U(z) > 0, R(z) > 0, W > 0 \text{ for } z \in [0, L_1]\Big\}.$$

Then $\mathcal{C}^* := \mathcal{C} \cap (\mathbb{R} \times P) \neq \phi$.

Let $\mathcal{C}^+$ be the component of $\mathcal{C} \setminus \{(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau)) : -\delta < \tau < 0\}$ containing $\{(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau)) : 0 \le \tau < \delta\}$ and $\mathcal{C}^-$ be the component of $\mathcal{C}\backslash\{(m_u(\tau), U(\tau,z), R(\tau,z), W(\tau)) : 0<\tau<\delta\}$ containing $\{(m_u(\tau), U(\tau,z), R(\tau, z), W(\tau)) : -\delta < \tau \leq 0\}$. It follows from Theorem 2.4 that each of $\mathcal{C}^+$ and $\mathcal{C}^-$ satisfies one of the following three cases:

(1) It is not compact in $\mathcal{X}$;
(2) It contains a point $(\tilde{m}_u, 0, W_{sed}, W_{sed})$ with $\tilde{m}_u \neq m_u^*$;
(3) It contains a point $(m_u, \tilde{U}(z), W_{sed}+\tilde{R}(z), W_{sed}+\tilde{W})$, where $0 \neq (\tilde{U}(z), \tilde{R}(z), \tilde{W}) \in Z$, Z is a closed complement of $\mathcal{N}(L) = \text{span}\{\Phi(z), \Psi(z), \Theta\}$ in $\mathcal{X}$.

Without loss of generality, we take

$$Z := \left\{(\tilde{U}(z), \tilde{R}(z), \tilde{W}) \in \mathcal{X} : \int_0^{L_1} [\tilde{U}(z)\Phi(z) + \tilde{R}(z)\Psi(z) + \tilde{W}\Theta]dz = 0\right\}, \quad (29)$$

where $\Phi(z), \Psi(z), \Theta$ are given in Theorem 3.1.

We only consider $\mathcal{C}^+$. From the strong maximum principle and connectedness of $\mathcal{C}^+$, all solutions $(U(z), R(z), W)$ of (4) on $\mathcal{C}^+$ satisfies $U(z) > 0$, $R(z) < W_{sed}$ and $W < W_{sed}$ from Lemma 3.2.

If case (2) holds, then $\mathcal{N}(\tilde{L}) \neq \{0\}$, where $\tilde{L} := F_{(U,R,W)}(\tilde{m}_u, 0, W_{sed}, W_{sed})$ for $\tilde{m}_u \neq m_u^*$. Indeed from Lemma 3.6 in [33], we must have $0 < \tilde{m}_u < m_u^*$. Then similar to (14)–(18), if $[\Phi(z), \Psi(z), \Theta] \in \mathcal{N}(\tilde{L})$, then we have

$$D_u\Phi''(z) - s\Phi'(z) + (m_u^* - \tilde{m}_u)\Phi(z) = 0, \quad D_u\Phi'(z) - s\Phi(z)|_{z=0,L_1} = 0,$$

and (16)–(18) still hold. Thus we must have $\Phi(z) = e^{\frac{sz}{2D_u}}\cos\left(\frac{k\pi z}{L_1}\right)$ for $k \in N$. Hence follow the same argument as in the proof of Theorem 3.1, we have the solutions of $F(m_u, U, R, W)$ near $(m_u, U, R, W) = (\tilde{m}_u, 0, W_{sed}, W_{sed})$ are in form

$$\{(m_u(\tau), U(\tau, z), R(\tau, z), W(\tau)) : \tau \in (-\delta, \delta)\},$$

where $m_u(0) = \tilde{m}_u$, $U(\tau, z) = \tau\Phi(z) + \tau g_1'(\tau, z)$, $R(\tau, z) = W_{sed} + \tau\Psi(z) + \tau g_2'(\tau, z)$, $W(\tau) = W_{sed} + \tau\Theta + \tau g_3'(\tau)$, and $g_i'(\tau, \cdot)(i = 1, 2)$, $g_3'(\tau)$ are given as in Theorem 3.1. But $U(\tau, z)$ is always sign-changing as $\Phi(z)$ is sign-changing. This contradicts with the assumption that any solution in $\mathcal{C}^+$ is positive. Hence case (2) cannot happen.

If case (3) holds, then there exists $\bar{m}_u \in (0, m_u^*)$, such that $(\tilde{U}(z), W_{sed} + \tilde{R}(z), W_{sed}+\tilde{W})$ is positive and it satisfies $F(\bar{m}_u, \tilde{U}(z), W_{sed}+\tilde{R}(z), W_{sed}+\tilde{W}) = 0$. From Lemma 3.2, we have $W_{sed} + \tilde{R}(z) < W_{sed}, W_{sed} + \tilde{W} < W_{sed}$ and $\tilde{U}(z) > 0$. Thus $\tilde{U}(z) > 0, \tilde{R}(z) < 0$ and $\tilde{W} < 0$ and it implies that

$$\int_0^{L_1} [\tilde{U}(z)\Phi(z) + \tilde{R}(z)\Psi(z) + \tilde{W}\Theta]dz > 0 \quad (30)$$

since $\Phi(z) > 0$, $\Psi(z) < 0$ and $\Theta < 0$ from the proof of Theorem 3.1. But (30) contradicts with (29), which implies that case (3) cannot happen either. Hence case (1) must occur for $\mathcal{C}^+$.

According to case (1), $\mathcal{C}^+$ is not compact in $\mathcal{X}$, which implies that it is unbounded in $\mathcal{X}$ by the elliptic regularity theory. By Lemma 3.2, if $m_u \in [\varepsilon, m_u^*)$ for any $\varepsilon > 0$, then $(U(z), R(z), W)$ is bounded. And also when $m_u = 0$, (4) has no positive solution. Thus, the projection of $\mathcal{C}^+$ on the m_u-axis must be the interval $(0, m_u^*)$, and as shown in Lemma 3.2, $||U||_\infty \to \infty$ as $m_u \to 0^+$. Now from Theorem 3.8 of [33], the positive solution of (4) is indeed unique and non-degenerate. Therefore $\mathcal{C}^+$ must be a smooth curve in form of (28) from the implicit function theorem, and $S^+ = \mathcal{C}^+$. □

Theorem 3.3 shows the continuous increase of the pelagic algae from 0 at $m_u = m_u^*$ to ∞ as $m_u = 0$, and the stability proved in Theorem 3.1 shows that this steady state E_3 is locally asymptotically stable near $m_u = m_u^*$ for the dynamics of (11) and the dynamics of (1) if m_v is large. The stability of E_3 for m_u not near the bifurcation point is still not known.

3.2. E_4 **bifurcating from** E_2 **at** $m_u = m_u^{**}$**.** In this subsection, we still use m_u as a bifurcation parameter, and consider the bifurcation of positive solution E_4 from the branch of semi-trivial solutions

$$\Gamma_{E_2} = \left\{ \left(m_u, 0, V_2 = \frac{b(W_{sed} - W_2)}{c_v m_v L_2(1-\beta_v)}, R_2 = \frac{\gamma_v m_v}{r_v - m_v}, W_2 = \frac{\gamma_v m_v}{r_v - m_v} \right) : m_u > 0 \right\}$$

at $m_u = m_u^{**}$. Let

$$\tilde{h} = c_u m_u^{**}(\beta_u - 1), \quad c_2 = \left[\frac{D_u^2 \tilde{h}}{s^2 D_r} + \frac{D_u \tilde{h}}{as} \right] e^{\frac{sL_1}{D_u}} - \left[\frac{D_u \tilde{h} L_1}{s D_r} + \frac{D_u \tilde{h}}{as} \right], \tag{31}$$

$$\tilde{\Psi}(z) = \frac{D_u \tilde{h}}{s D_r} z + c_2 - \frac{D_u^2 \tilde{h}}{s^2 D_r} e^{(s/D_u)z}, \tilde{\Phi}(z) = e^{(s/D_u)z}, \tilde{\Theta} = 0, \tilde{\Upsilon} = \frac{a \tilde{\Psi}(L_1)}{c_v m_v L_2 (1-\beta_v)}. \tag{32}$$

Theorem 3.4. *Assume that*

$$0 \le \beta_u, \beta_v < 1, \;\; 0 < m_u < m_u^{**}, \;\; 0 < m_v < \frac{r_v b W_{sed}}{\gamma_v (a+b) + b W_{sed}}. \tag{33}$$

Then there is a smooth curve Γ_{E_4} *of positive solutions of* (5) *bifurcating from the line of trivial solutions* $\{(m_u, 0, V_2, R_2, W_2)\}$ *at* $m_u = m_u^{**}$ *such that*

1. *near* $(m_u^{**}, 0, V_2, R_2, W_2)$*, there exists* $\delta > 0$ *such that all the positive solutions of* (5) *lie on a smooth curve*
$$\hat{\Gamma}_{E_4} = \{(m_u(\tau), U(\tau, z), V(\tau), R(\tau, z), W(\tau)) : 0 < \tau < \delta\},$$
where $U(\tau, z) = \tau \tilde{\Phi}(z) + \tau h_1(\tau, z), V(\tau) = V_2 + \tau \tilde{\Upsilon} + \tau h_2(\tau, z), R(\tau, z) = R_2(z) + \tau \tilde{\Psi}(z) + \tau h_3(\tau, z), W(\tau) = W_2 + \tau \tilde{\Theta} + \tau h_4(\tau)$*, and* $m_u(\tau), h_i(\tau, \cdot)(i = 1, 2, 3)$*,* $h_4(\tau)$ *are smooth functions defined for* $\tau \in (0, \delta)$ *such that* $m_u(0) = m_u^{**}$*,* $m_u'(0) < 0$*,* $h_i(0, \cdot) = 0 (i = 1, 2, 3)$ *and* $h_4(0) = 0$*;*
2. *for* $\tau \in (0, \delta)$*, the bifurcating solution* $(m_u(\tau), U(\tau, z), V(\tau), R(\tau, z), W(\tau))$ *is locally asymptotically stable with respect to* (1)*.*

Proof. Define a nonlinear mapping $G : \mathbb{R}^+ \times X_1 \times \mathbb{R} \times X_2 \times \mathbb{R} \to Y \times \mathbb{R} \times Y \times \mathbb{R} \times \mathbb{R}$ by

$$G(m_u, U(z), V, R(z), W) = \begin{pmatrix} D_u U''(z) - sU'(z) + \left(\dfrac{r_u R(z)}{R(z) + \gamma_u} - m_u \right) U(z) \\ \dfrac{r_v W V}{W + \gamma_v} - m_v V \\ D_r R''(z) + c_u \beta_u m_u U(z) - c_u \dfrac{r_u R(z)}{R(z) + \gamma_u} U(z) \\ b(W_{sed} - W) - a(W - R(L_1)) + c_v L_2 \left(\beta_v m_v - \dfrac{r_v W}{W + \gamma_v} \right) V \\ D_r R'(L_1) - a(W - R(L_1)) \end{pmatrix}. \tag{34}$$

By virtue of Theorem 3.11 in [33], (5) has a positive coexistence steady state E_4 under the condition (33). And it is easy to verify that $(V_2, R_2(z), W_2)$ is positive if and only if $0 \le \beta_v < 1, m_u > 0$ and $0 < m_v < r_v W_{sed}/(W_{sed} + \gamma_v)$. By linearizing the system (34) about a steady state $(\bar{U}(z), \bar{V}, \bar{R}(z), \bar{W})$, we get

$$G_{(U,V,R,W)}(m_u, \bar{U}(z), \bar{V}, \bar{R}(z), \bar{W})[\varphi(z), \xi, \phi(z), \zeta]$$
$$= \begin{pmatrix} D_u \varphi''(z) - s\varphi'(z) + \left(\dfrac{r_u \bar{R}(z)}{\bar{R}(z) + \gamma_u} - m_u \right) \varphi(z) + \dfrac{r_u \gamma_u \bar{U}(z)}{(\bar{R}(z) + \gamma_u)^2} \phi(z) \\ \left(\dfrac{r_v \bar{W}}{\bar{W} + \gamma_v} - m_v \right) \xi + \dfrac{r_v \gamma_v \bar{V}}{(\bar{W} + \gamma_v)^2} \zeta \\ \left(c_u \beta_u m_u - \dfrac{c_u r_u \bar{R}(z)}{\bar{R}(z) + \gamma_u} \right) \varphi(z) + D_r \phi''(z) - \dfrac{c_u r_u \gamma_u \bar{U}(z)}{(\bar{R}(z) + \gamma_u)^2} \phi(z) \\ \left(c_v \beta_v m_v - \dfrac{c_v r_v \bar{W}}{\bar{W} + \gamma_v} \right) \xi - \dfrac{c_v r_v \gamma_v \bar{V}}{(\bar{W} + \gamma_v)^2} \zeta + \dfrac{a}{L_2} \phi(L_1) - \dfrac{a+b}{L_2} \zeta \\ D_r \phi'(L_1) - a(\zeta - \phi(L_1)) \end{pmatrix}, \quad (35)$$

and by calculations, at $(m_u, \bar{U}(z), \bar{V}, \bar{R}(z), \bar{W}) = (m_u^{**}, 0, V_2, R_2(z), W_2)$, we have

$$G_{(U,V,R,W)}(m_u^{**}, 0, V_2, R_2(z), W_2)[\varphi(z), \xi, \phi(z), \zeta]$$
$$= \begin{pmatrix} D_u \varphi''(z) - s\varphi'(z) \\ \dfrac{r_v \gamma_v V_2}{(W_2 + \gamma_v)^2} \zeta \\ c_u m_u^{**} (\beta_u - 1) \varphi(z) + D_r \phi''(z) \\ c_v m_v (\beta_v - 1) \xi - \dfrac{c_v r_v \gamma_v V_2}{(W_2 + \gamma_v)^2} \zeta + \dfrac{a}{L_2} \phi(L_1) - \dfrac{a+b}{L_2} \zeta \\ D_r \phi'(L_1) - a(\zeta - \phi(L_1)) \end{pmatrix}. \quad (36)$$

We now prove that the conditions of Theorem 2.1 hold. First we have $G(m_u, 0, V_2, R_2(z), W_2) = 0$. Define

$$\tilde{L} := G_{(U,V,R,W)}(m_u^{**}, 0, V_2, R_2(z), W_2).$$

Suppose that $[\tilde{\Phi}(z), \tilde{\Upsilon}, \tilde{\Psi}(z), \tilde{\Theta}] \in \mathcal{N}(\tilde{L})$, then by (36), we get

$$D_u \tilde{\Phi}''(z) - s\tilde{\Phi}'(z) = 0, \quad D_u \tilde{\Phi}'(z) - s\tilde{\Phi}(z)|_{z=0,L_1} = 0, \quad (37)$$

$$\frac{r_v \gamma_v V_2}{(W_2 + \gamma_v)^2} \tilde{\Theta} = 0, \quad (38)$$

$$c_u m_u^{**} (\beta_u - 1) \tilde{\Phi}(z) + D_r \tilde{\Psi}''(z) = 0, \quad (39)$$

$$c_v m_v (\beta_v - 1) \tilde{\Upsilon} - \frac{c_v r_v \gamma_v V_2}{(W_2 + \gamma_v)^2} \tilde{\Theta} + \frac{a}{L_2} \tilde{\Psi}(L_1) - \frac{a+b}{L_2} \tilde{\Theta} = 0, \quad (40)$$

$$\tilde{\Psi}'(0) = 0, \quad D_r \tilde{\Psi}'(L_1) - a(\tilde{\Theta} - \tilde{\Psi}(L_1)) = 0. \quad (41)$$

Using the similar methods in Theorem 3.1, we have $\tilde{\Phi}(z) = e^{(s/D_u)z}$. From (38) and (41), we obtain $\tilde{\Theta} = 0$ and $D_r \tilde{\Psi}'(L_1) + a\tilde{\Psi}(L_1) = 0$. Combining the equation (39), $\tilde{\Psi}$ can be uniquely solved as (32) and (31). And thus, it follows from (40) and (32) that $\tilde{\Upsilon} = a\tilde{\Psi}(L_1)/[c_v m_v L_2(1 - \beta_v)]$. Hence $\dim \mathcal{N}(\tilde{L}) = 1$ and $\mathcal{N}(\tilde{L}) = \text{span}\{(\tilde{\Phi}(z), \tilde{\Upsilon}, \tilde{\Psi}(z), \tilde{\Theta})\}$. Carrying out our similar arguments as those in Theorem 3.1, we have

$$\mathcal{R}(\tilde{L}) = \left\{ (f_1, f_2, f_3, f_4, f_5)^\tau \in Y \times \mathbb{R} \times Y \times \mathbb{R} \times \mathbb{R} : \int_0^{L_1} f_1(z) dz = 0 \right\},$$

and codim$\mathcal{R}(L) = 1$. From (35), we have

$$G_{m_u(U,V,R,W)}(m_u^{**}, 0, V_2, R_2(z), W_2)[\tilde{\Phi}(z), \tilde{\Upsilon}, \tilde{\Psi}(z), \tilde{\Theta}] = \begin{pmatrix} -\tilde{\Phi}(z) \\ c_u\beta_u\tilde{\Phi}(z) \\ 0 \\ 0 \end{pmatrix}, \quad (42)$$

which yields that $G_{m_u(U,V,R,W)}(m_u^{**}, 0, V_2, R_2(z), W_2)[\tilde{\Phi}(z), \tilde{\Upsilon}, \tilde{\Psi}(z), \tilde{\Theta}] \notin \mathcal{R}(\tilde{L})$. Therefore all the conditions of Theorem 2.1 hold.

From Theorem 2.1, we conclude that the solution set of (5) near $(m_u^{**}, 0, V_2, R_2(z), W_2)$ consists precisely of the curves

$$\hat{\Gamma}_{E_2} = \{(m_u, 0, V_2, R_2(z), W_2) : m_u > 0\}$$

and

$$\hat{\Gamma}_{E_4} = \{(m_u(\tau), U(\tau, z), V(\tau), R(\tau, z), W(\tau)) : 0 < \tau < \delta\}.$$

Here $U(\tau, z) = \tau\tilde{\Phi} + \tau h_1(\tau, z), V(\tau) = V_2 + \tau\tilde{\Upsilon} + \tau h_2(\tau, z), R(\tau, z) = R_2(z) + \tau\tilde{\Psi} + \tau h_3(\tau, z), W(\tau) = W_2 + \tau\tilde{\Theta} + \tau h_4(\tau)$ such that $m_u(0) = m_u^{**}$, $h_i(0, \cdot) = 0(i = 1, 2, 3), h_4(0) = 0$ and

$$\begin{aligned} m_u'(0) =& -\frac{\left\langle \tilde{l},\ G_{(U,V,R,W)(U,V,R,W)}(m_u^{**}, 0, V_2, R_2(z), W_2)[\tilde{\Phi}(z), \tilde{\Upsilon}, \tilde{\Psi}(z), \tilde{\Theta}]^2 \right\rangle}{2\left\langle \tilde{l},\ G_{m_u(U,V,R,W)}(m_u^{**}, 0, V_2, R_2(z), W_2)[\tilde{\Phi}(z), \tilde{\Upsilon}, \tilde{\Psi}(z), \tilde{\Theta}] \right\rangle} \\ =& -\frac{\int_0^{L_1} \frac{2r_u\gamma_u(r_v - m_v)^2}{[\gamma_v m_v + \gamma_u(r_v - m_v)]^2}\tilde{\Phi}(z)\tilde{\Psi}(z)dz}{-2\int_0^{L_1} e^{\frac{sz}{D_u}}dz}, \end{aligned} \quad (43)$$

where $\tilde{l}$ is a linear functional on $Y \times \mathbb{R} \times Y \times \mathbb{R} \times \mathbb{R}$ satisfying $\mathcal{N}(\tilde{l}) = \mathcal{R}(\tilde{l})$. It follows from (33) and (31) that $\tilde{h} < 0$, which implies $\tilde{\Psi}(z)$ is nondecreasing in z, and so $\tilde{\Psi}(z) < 0$ on $[0, L_1]$. Furthermore, by (43), we derive that $m_u'(0) < 0$. This completes the proof of part 1.

By Theorem 2.2, we see that there exist continuously differentiable functions $\gamma : (m_u^{**} - \varepsilon, m_u^{**} + \varepsilon) \to \mathbb{R}$, $[\hat{\varphi}, \hat{\xi}, \hat{\phi}, \hat{\zeta}] : (m_u^{**} - \varepsilon, m_u^{**} + \varepsilon) \to X_1 \times \mathbb{R} \times X_2 \times \mathbb{R}$, $\mu : (-\delta, \delta) \to \mathbb{R}$ and $[\varphi^*, \xi^*, \phi^*, \zeta^*] : (-\delta, \delta) \to X_1 \times \mathbb{R} \times X_2 \times \mathbb{R}$ such that

$$\begin{aligned} &G_{(U,V,R,W)}(m_u, 0, V_2, R_2(z), W_2)[\hat{\varphi}(m_u), \hat{\xi}(m_u), \hat{\phi}(m_u), \hat{\zeta}(m_u)] \\ =&\gamma(m_u)[\hat{\varphi}(m_u), \hat{\xi}(m_u), \hat{\phi}(m_u), \hat{\zeta}(m_u), 0]^T, \end{aligned} \quad (44)$$

$$\begin{aligned} &G_{(U,V,R,W)}(m_u(\tau), U(\tau), V(\tau), R(\tau), W(\tau))[\varphi^*(\tau), \xi^*(\tau), \phi^*(\tau), \zeta^*(\tau)] \\ =&\mu(\tau)[\varphi^*(\tau), \xi^*(\tau), \phi^*(\tau), \zeta^*(\tau), 0]^T. \end{aligned} \quad (45)$$

It follows from (35) that $\gamma(m_u) = m_u^{**} - m_u$ and it is easy to see that $\gamma'(m_u) = -1$. Moreover $\gamma(m_u^{**}) = 0$ is the principal eigenvalue of $G_{(U,V,R,W)}(m_u, 0, V_2, R_2(z), W_2)$, hence the perturbed eigenvalue $\mu(\tau)$ is also the eigenvalue of $G_{(U,V,R,W)}(m_u(\tau), U(\tau), V(\tau), R(\tau), W(\tau))$. Together with $m_u'(0) < 0$, we have $\mu(\tau) < 0$ for sufficiently small $\tau > 0$, and so the bifurcating solution $(m_u(\tau), U(\tau, z), V(\tau), R(\tau, z), W(\tau))$ is locally asymptotically stable with respect to (1). This completes the proof of part 2. □

It follows from Lemma 3.10 in [33] and similar arguments in Lemma 3.2, we obtain the following *a priori* estimates for positive solutions (U_4, V_4, R_4, W_4) of (5).

Lemma 3.5. *Assume that* $(U_4, V_4, R_4, W_4) \in C([0, L_1]) \times \mathbb{R}_+ \times C([0, L_1]) \times \mathbb{R}_+$ *is a positive solution of* (5) *and* $\beta_u \in [0, 1)$. *Then*

(i) $\dfrac{\beta_u \gamma_u m_u}{r_u - \beta_u m_u} \le R_4(z) < \dfrac{\gamma_v m_v}{r_v - m_v}$ *for all* $z \in [0, L_1]$;
(ii) *for any* $\varepsilon > 0$, *there exists a positive constant* $B(\varepsilon)$ *such that* $\|U_4\|_\infty \le B(\varepsilon)$ *if* $m_u \in [\varepsilon, m_u^{**})$, *and* $\|U_4^{m_u}\|_\infty \to \infty$ *as* $m_u \to 0$.

By applying Lemma 3.5 and similar arguments as in Theorem 3.3, we have the following conclusion.

Theorem 3.6. *Let* $\tilde{S}^+$ *be the set of positive solutions to* (5). *Then* $\tilde{S}^+$ *is a smooth curve in* $\mathbb{R}^+ \times \mathcal{X}$ *in form*

$$\tilde{S}^+ = \{(m_u, U_4(m_u, z), V_4(m_u, z), R_4(m_u, z), W_4(m_u)) : 0 < m_u < m_u^{**}\} \tag{46}$$

satisfying $\lim_{m_u \to (m_u^{**})^-} (U_4(m_u, \cdot), V_4(m_u), R_4(m_u, \cdot), W_4(m_u)) = (0, V_2, R_2(z), W_2)$, *and* $\lim_{m_u \to 0^+} \|U_4(m_u, \cdot)\|_\infty = \infty$.

We now prove the part 3 of Theorem 3.1 by using the setting in the proof of Theorem 3.4.

Proof of Theorem 3.1 part 3. We assume that $m_v > r_v W_{sed}/(W_{sed} + \gamma_v)$. Now similar to the proof of Theorem 3.4 part 2, the stability of the bifurcating solution $E_3(\tau) = (m_u(\tau), U_3(\tau, z),\ 0, R_3(\tau, z), W_3(\tau))$ can be determined by the linearized eigenvalue problems:

$$\begin{aligned} &G_{(U,V,R,W)}\,(m_u, 0, 0, W_{sed}, W_{sed})\,[\tilde{\varphi}(m_u), \tilde{\xi}(m_u), \tilde{\phi}(m_u), \tilde{\zeta}(m_u)] \\ =&\tilde{\gamma}(m_u)[\tilde{\varphi}(m_u), \tilde{\xi}(m_u), \tilde{\phi}(m_u), \tilde{\zeta}(m_u), 0]^T, \end{aligned} \tag{47}$$

$$\begin{aligned} &G_{(U,V,R,W)}\,(m_u(\tau), U_3(\tau), 0, R_3(\tau), W_3(\tau))\,[\varphi^{**}(\tau), \xi^{**}(\tau), \phi^{**}(\tau), \zeta^{**}(\tau)] \\ =&\tilde{\mu}(\tau)[\varphi^{**}(\tau), \xi^{**}(\tau), \phi^{**}(\tau), \zeta^{**}(\tau), 0]^T, \end{aligned} \tag{48}$$

where $\tilde{\gamma} : (m_u^* - \varepsilon, m_u^* + \varepsilon) \to \mathbb{R}$, $[\tilde{\varphi}, \tilde{\xi}, \tilde{\phi}, \tilde{\zeta}] : (m_u^* - \varepsilon, m_u^* + \varepsilon) \to X_1 \times \mathbb{R} \times X_2 \times \mathbb{R}$, $\mu : (-\delta, \delta) \to \mathbb{R}$ and $[\varphi^{**}, \xi^{**}, \phi^{**}, \zeta^{**}] : (-\delta, \delta) \to X_1 \times \mathbb{R} \times X_2 \times \mathbb{R}$ are continuously differentiable functions. Then the second equation in (48) at $m_u = m_u^*$ becomes

$$\left(\frac{r_v W_{sed}}{W_{sed} + \gamma_v} - m_v \right) \xi = \tilde{\gamma}(m_u)\xi. \tag{49}$$

Since $m_v > r_v W_{sed}/(W_{sed}+\gamma_v)$, we must have $\xi = 0$ when $m_u = m_u^*$. Then the principal eigenvalue of $G_{(U,V,R,W)}\,(m_u^*, 0, 0, W_{sed}, W_{sed})$ is $\tilde{\gamma}(m_u^*) = 0$ with eigenfunction $[\Phi(z), 0, \Psi(z), \Theta]$, where $[\Phi(z), \Psi(z), \Theta]$ is defined by (15)-(18). Now following the same argument as in proof of the Theorem 3.1 part 2, we conclude that $\tilde{\mu}(\tau) < 0$ which implies the local asymptotic stability of $E_3(\tau)$. □

Remark 3.2. If $\beta_u = \beta_v = 1$, then from (1), we have

$$\frac{d}{dt} \int_0^{L_1} (c_u U + R) dz = D_r R_z|_0^{L_1} = a(W - R(L_1)) \tag{50}$$

and

$$\frac{d}{dt} \int_0^{L_1} (c_v V + W) dz = \frac{b}{L_2}(W_{sed} - W) - \frac{a}{L_2}(W - R(L_1)). \tag{51}$$

Adding (50) and (51) together, we get

$$\frac{d}{dt} \int_0^{L_1} \left[(c_u U + R) + L_2(c_v V + W) \right] dz = b(W_{sed} - W). \tag{52}$$

When considering the steady state solutions, (52) implies that $W = W_{sed}$, and thus by (50), we know $R(L_1) = W$.

By adding the equations and the boundary conditions of U and R in (5), we have

$$\begin{cases} c_u D_u U_{zz} - c_u s U_z + D_r R_{zz} = 0, & 0 < z < L_1, \\ c_u(D_u U_z - sU) + D_r R_z = 0, & z = 0,\ L_1, \end{cases} \tag{53}$$

and so

$$c_u(D_u U_z - sU) + D_r R_z = 0, \quad z \in [0, L_1]. \tag{54}$$

It follows from Lemma 3.6 in [33] that $D_u U_z - sU \geq 0$ and $R_z \geq 0$ for $z \in [0, L_1]$. This and (54) imply that $D_u U_z - sU = 0,\ \forall\ z \in [0, L_1]$ and $R_z = 0, \forall\ z \in [0, L_1]$. Hence $R(z) \equiv W_{sed}$.

In addition, integrating the first equation in (5), we have

$$\int_0^{L_1} \left(m_u U - \frac{r_u R U}{R + \gamma_u} \right) dz = 0. \tag{55}$$

By $0 < m_u < \frac{r_u W_{sed}}{W_{sed} + \gamma_u}$ and (55), we have $U(z) \equiv 0$, and then we see $V = 0$ from (5). We show that when $\beta_u = \beta_v = 1$, then the only equilibrium is $(0, 0, W_{sed}, W_{sed})$ which is E_1.

4. **Asymptotic behavior of positive steady states.**

This section focuses on the limiting profiles of positive solutions of (5) when the diffusion coefficients are sufficiently small and large, respectively.

Let $D_r = M D_u$, $M \in \mathbb{R}^+$, $D = D_u$, $\tilde{c_u} = c_u/M$ and $\tilde{a} = a/M$. It follows from Theorem 3.11 in [33] that if (33) holds, then (5) has a unique positive coexistence steady state

$$\left(U_D(z), V_D = \frac{b(W_{sed} - W_D) + a(W_D - R_D(L_1))}{c_v m_v L_2 (1 - \beta_v)}, R_D(z), W_D = \frac{\gamma_v m_v}{r_v - m_v} \right),$$

which satisfies the following system

$$\begin{cases} -DU''(z) + sU'(z) = \left(\dfrac{r_u R(z)}{R(z) + \gamma_u} - m_u \right) U(z), & 0 < z < L_1, \\ \dfrac{r_v W}{W + \gamma_v} - m_v = 0, & \\ -DR''(z) = -\tilde{c_u} \left(\dfrac{r_u R(z)}{R(z) + \gamma_u} - \beta_u m_u \right) U(z), & 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) + c_v L_2 \left(\beta_v m_v - \dfrac{r_v W}{W + \gamma_v} \right) V = 0, & \\ DU'(0) - sU(0) = DU'(L_1) - sU(L_1) = 0, & \\ R'(0) = 0, \quad DR'(L_1) = \tilde{a}(W - R(L_1)). & \end{cases} \tag{56}$$

In the rest of this section, we always assume that the conditions (33) holds.

4.1. **Small diffusion case when $s > 0$.**

In this subsection, we always assume that $s > 0$. We choose $z_D \in [0, L_1]$ such that $U_D(z_D) = \max_{z \in [0, L_1]} U_D(z) = \|U_D\|_\infty$. Set

$$\bar{U}_D(z) := U_D(z) \exp\left[-s(z - z_D)/(2D) \right].$$

Then $(\bar{U}_D, R_D)$ satisfies the system

$$\begin{cases} -D\bar{U}''(z) + \dfrac{s^2}{4D}\bar{U}(z) = \left(\dfrac{r_u R(z)}{R(z)+\gamma_u} - m_u\right)\bar{U}(z), & 0 < z < L_1, \\ -DR''(z) = -\tilde{c_u}\left(\dfrac{r_u R(z)}{R(z)+\gamma_u} - \beta_u m_u\right)\bar{U}(z)e^{\frac{s(z-z_D)}{2D}}, & 0 < z < L_1, \\ \bar{U}'(0) = \dfrac{s}{2D}\bar{U}(0), \quad \bar{U}'(L_1) = \dfrac{s}{2D}\bar{U}(L_1), \\ R'(0) = 0, \quad R'(L_1) = \dfrac{\tilde{a}}{D}\left(\dfrac{\gamma_v m_v}{r_v - m_v} - R(L_1)\right). \end{cases} \tag{57}$$

Let

$$z = z_D + Dy,\ \check{U}_D(y) = \bar{U}_D(z_D + Dy) \text{ and } \check{R}_D(y) = R_D(z_D + Dy).$$

Then (57) can be reformulated as

$$\begin{cases} -\check{U}''(y) + \dfrac{s^2}{4}\check{U}(y) = D\left(\dfrac{r_u\check{R}(y)}{\check{R}(y)+\gamma_u} - m_u\right)\check{U}(y), & -\dfrac{z_D}{D} < y < \dfrac{L_1 - z_D}{D}, \\ -\check{R}''(y) = -D\tilde{c_u}\left(\dfrac{r_u\check{R}(y)}{\check{R}(y)+\gamma_u} - \beta_u m_u\right)\check{U}(y)e^{\frac{sy}{2}}, & -\dfrac{z_D}{D} < y < \dfrac{L_1 - z_D}{D}, \\ \check{U}'(y) = \dfrac{s}{2}\check{U}(y), \quad y = -z_D/D, \quad (L_1 - z_D)/D, \\ \check{R}'(-z_D/D) = 0, \quad \check{R}'((L_1 - z_D)/D) = \tilde{a}\left[\dfrac{\gamma_v m_v}{r_v - m_v} - \check{R}((L_1 - z_D)/D)\right]. \end{cases} \tag{58}$$

It follows from Lemma 3.10 in [33] that $U_D(z)$ is strictly increasing on $z \in (0, L_1)$ if $s > 0$. Note that the function $r_u\check{R}(y)/(\check{R}(y) + \gamma_u) - m_u$ is uniformly bounded for all $y \in [-z_D/D, (L_1 - z_D)/D]$ and $0 < m_u < m_u^{**}$.

We now explore the asymptotic behavior of $U_D(z)$ and $R_D(z)$ in the case of small diffusion coefficient D. From the equation and boundary conditions of $\check{U}_D$ in (58) and similar arguments as Lemma 3.1 in [17], we have

Lemma 4.1. *There exists $D_0 > 0$ such that for any $0 < D < D_0$, $U_D(z)$ is strictly increasing on $[0, L_1]$ and $z_D = L_1$.*

In the remaining part of this subsection, we always assume that $0 < D < D_0$. Let

$$\tilde{U}_D(y) = \frac{\check{U}_D(y)}{\|\check{U}_D\|_\infty}, \quad y \in [-L_1/D, 0].$$

Then we have $\|\tilde{U}_D\|_\infty = \tilde{U}_D(L_1) = 1$ and define

$$\hat{U}_D(z) := D^{-1}\frac{\bar{U}_D(z)}{\|\bar{U}_D\|_\infty}\exp\left[\frac{s}{2D}(z - L_1)\right] = D^{-1}\frac{U_D(z)}{\|\bar{U}_D\|_\infty}. \tag{59}$$

By means of the similar methods of proof as Lemmas 3.2–3.4 in [17], we obtain

Theorem 4.2. *The following conclusions hold:*

(i) *$\tilde{U}_D(y) \to \exp(sy/2)$ on $C^1_{loc}((-\infty, 0])$ as $D \to 0$;*
(ii) *$\left\|\bar{U}_D(z)/\|\bar{U}_D\|_\infty - \exp[s(z - L_1)/(2D)]\right\|_\infty \to 0$ as $D \to 0$;*
(iii) *for any $\delta \in (0, L_1)$ and $z \in [0, \delta]$, we have*

$$0 < \hat{U}_D(z) \le D^{-1}\exp[s(\delta - 1)/(2D)] \to 0 \text{ as } D \to 0,$$

and

$$\lim_{D\to 0}\int_0^{L_1}\hat{U}_D(z)dz = \frac{1}{s}.$$

Let $\tau_D := D\|\bar{U}_D\|_\infty$. Then we have

Lemma 4.3. *If $m_u \in [\varepsilon, m_u^{**})$ for any $\varepsilon > 0$, then $\limsup_{D\to 0}\tau_D < \infty$.*

Proof. Assume that there exists a sequence of D, denoted by D_n, such that $D_n \to 0$ and $\tau_n := \tau_{D_n} \to \infty$. Let $\hat{U}_n := \hat{U}_{D_n}, R_n := R_{D_n}$. From (59), we get $\hat{U}_n(z) = U_n(z)/\tau_n$ and

$$\begin{cases} -D_n\hat{U}_n''(z) + s\hat{U}_n'(z) = \left(\dfrac{r_uR_n(z)}{R_n(z)+\gamma_u} - m_u\right)\hat{U}_n(z), \quad 0 < z < L_1, \\ D_n\hat{U}_n'(0) - s\hat{U}_n(0) = D_n\hat{U}_n'(L_1) - s\hat{U}_n(L_1) = 0. \end{cases} \tag{60}$$

Integrating (60) on $[0, L_1]$ gives

$$\int_0^{L_1}\left(\frac{r_uR_n(z)}{R_n(z)+\gamma_u} - m_u\right)\hat{U}_n(z)dz = 0.$$

It follows from Lemma 3.5 that $\|U_n\|_\infty \le B(\varepsilon)$ if $m_u \in [\varepsilon, m_u^{**})$, thus we have

$$\begin{aligned} m_u\int_0^{L_1}\hat{U}_n(z)dz &= \int_0^{L_1}\frac{r_uR_n(z)}{R_n(z)+\gamma_u}\hat{U}_n(z)dz \\ &\le \int_0^{L_1} r_u\frac{1}{\tau_n}U_n(z)dz \le r_u\frac{1}{\tau_n}\|U_n\|_\infty \le r_u\frac{1}{\tau_n}B(\varepsilon). \end{aligned}$$

By Theorem 4.2, we have $\lim_{n\to\infty}\int_0^{L_1}\hat{U}_n(z)dz = 1/s$. This leads to

$$\limsup_{n\to\infty}\tau_n \le \frac{sr_u}{m_u}B(\varepsilon),$$

which contradicts with our assumption $\tau_n \to \infty$. The contradiction finishes the proof. □

Now we obtain the asymptotic limit of $R_D(z)$ as the diffusion parameter $D \to 0$.

Theorem 4.4. *Suppose that $s > 0$ and $m_u \in [\varepsilon, m_u^{**})$ for some small $\varepsilon > 0$, then $\lim_{D\to 0}R_D(z) = \dfrac{\gamma_v m_v}{r_v - m_v}$ uniformly on $[0, L_1]$.*

Proof. From Lemmas 4.2 and 4.3, we have

$$D^{-1}U_D(z) = D^{-1}\hat{U}_D(z)\tau_D \le D^{-2}\exp\left[s(\delta-1)/(2D)\right]\tau_D \to 0$$

uniformly on any compact subset of $[0, L_1)$ as $D \to 0$. It follows from (56) that R_D satisfies

$$\begin{cases} -R_D''(z) = -\tilde{c_u}\left(\dfrac{r_uR_D(z)}{R_D(z)+\gamma_u} - \beta_u m_u\right)D^{-1}U_D(z), \quad 0 < z < L_1, \\ R_D'(0) = 0, \quad DR_D'(L_1) = \tilde{a}\left(\dfrac{\gamma_v m_v}{r_v - m_v} - R_D(L_1)\right). \end{cases} \tag{61}$$

By Lemma 3.10 in [33], we note that $R_D(z)$ is strictly increasing on $[0, L_1]$ and $\beta_u\gamma_u m_u/(r_u - \beta_u m_u) \le R_D(z) < \gamma_v m_v/(r_v - m_v)$ for all $z \in [0, L_1]$, thus $0 < r_uR_D(z)/(R_D(z)+\gamma_u) - \beta_u m_u < m_u^{**}$ for all $z \in [0, L_1]$ and $R_D''(z) \ge 0$ on $(0, L_1)$.

Note that the right hand side of the first equation in (61) tends to 0 uniformly in any compact subset of $[0, L_1)$ as $D \to 0$. It follows from the elliptic theory and the diagonal argument that there exists a C^1 convergent subsequence of $R_D(z)$, denoted by $R_n(z) = R_{D_n}(z)$, such that $R_n(z) \to R_0(z)$ in $C^1([0,\delta])$ for any $\delta \in (0, L_1)$ as $n \to \infty$. From (61), $R_0(z)$ satisfies

$$R_0''(z) = 0 \quad \text{for } z \in (0, L_1), \ \ R_0'(0) = 0.$$

Thus $R_0(z) = \tilde{C}$ (a constant) for any $z \in [0, L_1]$. An elementary argument shows that $R_n(z) \to R_0(z)$ uniformly in any compact subset of $[0, L_1)$. Moreover integrating the first equation in (61) on $[0, L_1]$, and observing that the right hand side of the first equation in (61) tends to 0, we obtain that $R_n'(z)$ is small for $z \in [0, L_1)$ which implies that $R_n(L_1) - R_n(0)$ is small as $n \to \infty$. Hence $R_n(z) \to R_0(z)$ uniformly in $[0, L_1]$ as $n \to \infty$. Thus we have

$$\begin{aligned}\tilde{C} =& R_0(L_1) = \lim_{n\to\infty} R_n(L_1) = \lim_{n\to\infty}\left[\frac{\gamma_v m_v}{r_v - m_v} - \frac{D_n}{\tilde{a}} R_n'(L_1)\right]\\ =& \frac{\gamma_v m_v}{r_v - m_v} - \frac{1}{\tilde{a}} \lim_{n\to\infty} D_n R_n'(L_1)\\ =& \frac{\gamma_v m_v}{r_v - m_v} - \frac{1}{\tilde{a}} \lim_{n\to\infty} D_n \lim_{n\to\infty} \int_0^{L_1} \tilde{c_u}\left(\frac{r_u R_n(z)}{R_n(z)+\gamma_u} - \beta_u m_u\right) D_n^{-1} U_n(z) dz\\ =& \frac{\gamma_v m_v}{r_v - m_v},\end{aligned}$$

where the last equality follows from the Lebesgue dominated convergence theorem. This completes the proof. □

4.2. **Small diffusion case when $s < 0$.** In this subsection we always assume that $s < 0$, and we still consider the system (56) with the positive coexistence steady state $(U_D(z), V_D, R_D(z), W_D)$. Here $\bar{U}_D(z), \check{U}_D(y), \check{R}_D(y)$ are defined in the same way as in the subsection 3.1, and $(\bar{U}_D, R_D)$ and $(\check{U}_D, \check{R}_D)$ satisfy the systems (57) and (58), respectively.

By means of the similar method as Lemma 3.10 in [17], we have

Lemma 4.5. *There exists $D_0 > 0$ such that for any $0 < D < D_0$, $U_D(z)$ is strictly decreasing in $[0, L_1]$ and $z_D = 0$.*

In the following, we always assume that $0 < D < D_0$. Let

$$\begin{aligned}&\tilde{U}_D(y) = \frac{\check{U}_D(y)}{\|\check{U}_D\|_\infty}, y \in [0, L_1/D], \ \tau_D = D\|\bar{U}_D\|_\infty,\\ &\hat{U}_D(z) = D^{-1}\frac{\bar{U}_D(z)}{\|\bar{U}_D\|_\infty} e^{\frac{s}{2D}z} = D^{-1}\frac{U_D(z)}{\|\bar{U}_D\|_\infty},\end{aligned}$$

Then $\|\tilde{U}_D\|_\infty = \tilde{U}_D(0) = 1$. Carrying out similar arguments as Lemma 3.11–3.13 in [17], we obtain

Theorem 4.6. *The following conclusions hold:*

(i) $\tilde{U}_D(y) \to \exp(sy/2)$ *in* $C^1_{loc}(([0,\infty))$ *as* $D \to 0$*;*
(ii) $\left\|\bar{U}_D(x)/\|\bar{U}_D\|_\infty - \exp(sz/(2D))\right\|_\infty \to 0$ *as* $D \to 0$*;*
(iii) *for any* $\delta \in (0, L_1)$ *and* $z \in [\delta, 1]$*, we have*

$$0 < \hat{U}_D(z) \le D^{-1}\exp[-s|\delta|/(2D)] \to 0 \ \text{ as } D \to 0,$$

and

$$\lim_{D\to 0}\int_0^{L_1} \hat{U}_D(z)dz = \frac{1}{|s|};$$

(iv) *if* $m_u \in [\varepsilon, r_u\gamma_v m_v/(\gamma_v m_v+\gamma_u r_v-\gamma_u m_v))$ *for any* $\varepsilon > 0$*, then* $\limsup_{D\to 0} \tau_D < \infty$.

Now we have the following result on the asymptomatic behavior of the coexistence state as $D \to 0$ when $s < 0$.

Theorem 4.7. *Suppose that* $s < 0$*. If* $m_u \in [\varepsilon, r_u\gamma_v m_v/(\gamma_v m_v + \gamma_u r_v - \gamma_u m_v))$ *for any* $\varepsilon > 0$*, then*

$$\lim_{D\to 0} R_D(z) = \frac{1}{L_1}\left(\frac{\gamma_v m_v}{r_v - m_v} - \frac{\gamma_u m_u}{r_u - m_u}\right)(z - L_1) + \frac{\gamma_v m_v}{r_v - m_v}$$

uniformly in $[0, L_1]$.

Proof. By Theorem 4.6, we have $D^{-1}U_D(z) \to 0$ uniformly on any compact subset of $(0, L_1]$ as $D \to 0$. Note that R_D satisfies equation (61) and the right side of the first equation in (61) tends to 0 uniformly in any compact subset of $(0, L_1]$ as $D \to 0$. It follows from the elliptic equation theory and the diagonal argument that there exists a sequence of D, denoted by D_n, such that $R_n(z) := R_{D_n}(z) \to R_0(z)$ in $C^1([\varepsilon, L_1])$ for any $\varepsilon \in (0, L_1)$ as $D_n \to 0$. From (61), we have

$$R_0''(z) = 0 \text{ for } z \in (0, L_1),\ R_0(L_1) = \frac{\gamma_v m_v}{r_v - m_v},$$

which implies that

$$R_0(z) = \hat{c}(z - L_1) + \frac{\gamma_v m_v}{r_v - m_v}$$

for some constant $\hat{c}$. An elementary argument shows that $R_n(z) \to R_0(z)$ uniformly in any compact subset of $(0, L_1]$, which implies $R_n(z) \to R_0(z)$ uniformly in $[0, L_1]$. Integrating (60) on $[0, L_1]$ gives

$$\int_0^{L_1} \left(\frac{r_u R_n(z)}{R_n(z) + \gamma_u} - m_u\right) \hat{U}_n(z)dz = 0.$$

By Theorem 4.6, as $n \to \infty$, we have

$$\int_0^{L_1} \hat{U}_n(z)dz \to 1/|s|,\ \int_\varepsilon^{L_1} \hat{U}_n(z)dz \to 0,$$
$$\Big|\int_\varepsilon^{L_1} \frac{r_u R_n(z)}{R_n(z) + \gamma_u}\hat{U}_n(z)dz\Big| \le \int_\varepsilon^{L_1} r_u\hat{U}_n(z)dz \to 0$$

for small $\varepsilon \in (0, 1)$. Hence, we deduce

$$\begin{aligned} m_u \int_0^\varepsilon \hat{U}_n(z)dz =& \int_0^\varepsilon \frac{r_u R_n(z)}{R_n(z) + \gamma_u}\hat{U}_n(z)dz + o_n(1) \\ =&[1 + o_\varepsilon(1)]\frac{r_u\left(\frac{\gamma_v m_v}{r_v - m_v} - \hat{c}L_1\right)}{\left(\frac{\gamma_v m_v}{r_v - m_v} - \hat{c}L_1\right) + \gamma_u} \int_0^\varepsilon \hat{U}_n(z)dz + o_n(1). \end{aligned}$$

Letting $n \to \infty$ and then letting $\varepsilon \to 0$, we have

$$\frac{m_u}{|s|} = \frac{r_u\left[\gamma_v m_v - \hat{c}L_1(r_v - m_v)\right]}{\left[\gamma_v m_v + (\gamma_u - \hat{c}L_1)(r_v - m_v)\right]} \cdot \frac{1}{|s|},$$

from which, we obtain

$$\hat{c} = \frac{1}{L_1}\left(\frac{\gamma_v m_v}{r_v - m_v} - \frac{\gamma_u m_u}{r_u - m_u}\right).$$

This completes the proof. □

4.3. **The large diffusion case.** In this subsection, we consider the limiting profile of the coexistence steady state as the diffusion coefficient $D \to \infty$. Let $\tilde{U}_D(z) = U_D(z)e^{-sz/(2D)}$ for $z \in [0, L_1]$. In the case of large diffusion, we have the following conclusion.

Theorem 4.8. *$\tilde{U}_D/\|\tilde{U}_D\|_\infty \to 1$ and $R_D(z) \to m_u\gamma_u/(r_u - m_u)$ uniformly in $[0, L_1]$ when $D \to \infty$.*

Proof. Note that $(\tilde{U}_D(z), R_D(z))$ satisfies

$$\begin{cases} -\tilde{U}_D'' + \dfrac{s^2}{4D^2}\tilde{U}_D = \dfrac{1}{D}\left(\dfrac{r_u R_D}{R_D + \gamma_u} - m_u\right)\tilde{U}_D, & 0 < z < L_1, \\ -R_D'' = -\dfrac{\tilde{c_u}}{D}\left(\dfrac{r_u R_D}{R_D + \gamma_u} - \beta_u m_u\right)e^{sz/(2D)}\tilde{U}_D, & 0 < z < L_1, \\ \tilde{U}_D'(0) - \dfrac{s}{2D}\tilde{U}_D(0) = \tilde{U}_D'(L_1) - \dfrac{s}{2D}\tilde{U}_D(L_1) = 0, \\ R_D'(0) = 0, \quad R_D'(L_1) = \dfrac{\tilde{a}}{D}\left(\dfrac{\gamma_v m_v}{r_v - m_v} - R_D(L_1)\right). \end{cases} \tag{62}$$

Let $\hat{U}_D = \tilde{U}_D/\|\tilde{U}_D\|_\infty$. Then, from (62) we get

$$\begin{cases} -\hat{U}_D'' + \dfrac{s^2}{4D^2}\hat{U}_D = \dfrac{1}{D}\left(\dfrac{r_u R_D}{R_D + \gamma_u} - m_u\right)\hat{U}_D, & 0 < z < L_1, \\ -R_D'' = -\dfrac{\tilde{c_u}}{D}\left(\dfrac{r_u R_D}{R_D + \gamma_u} - \beta_u m_u\right)e^{sz/(2D)}\tilde{U}_D, & 0 < z < L_1, \\ \tilde{U}_D'(0) - \dfrac{s}{2D}\tilde{U}_D(0) = \tilde{U}_D'(L_1) - \dfrac{s}{2D}\tilde{U}_D(L_1) = 0, \\ R_D'(0) = 0, \quad R_D'(L_1) = \dfrac{\tilde{a}}{D}\left(\dfrac{\gamma_v m_v}{r_v - m_v} - R_D(L_1)\right). \end{cases} \tag{63}$$

It is clear that $\hat{U}_D$ and $\hat{U}_D''$ are both uniformly bounded on $[0, L_1]$ for all large D. Then we choose a sequence, say D_n, such that $D_n \to \infty$, and $\hat{U}_n := \hat{U}_{D_n}$ converges to a function U_* in $C^1([0, L_1])$, and U_* satisfies (in the weak then the classical sense)

$$U_*'' = 0 \quad \text{in} \quad (0, L_1), \qquad U_*'(0) = U_*'(L_1) = 0, \qquad \|U_*\|_\infty = 1,$$

which implies $U_* \equiv 1$. Hence $\hat{U}_D \to 1$ in $C^1([0, L_1])$ as $D \to \infty$.

It is clear that $\|\tilde{U}_D\|_\infty$ is bounded away from ∞ for large D. It follows from the second and fourth equation of (63) that there exists a subsequence, say D_n, such that $D_n \to \infty$, and $R_n := R_{D_n}$ converges to a function R_* in $C^1([0, L_1])$, and R_* satisfies (in the weak then classical sense)

$$R_*'' = 0 \quad \text{in} \quad (0, L_1), \qquad R_*'(0) = 0, \qquad R_*'(L_1) = 0,$$

which implies $R_* =$ constant. Multiplying the first equation in (63) by $e^{sz/(2D)}$ and then integrating on $[0, L_1]$, we have

$$\int_0^{L_1} \left[\frac{r_u R_D(z)}{R_D(z) + \gamma_u} - m_u\right]\hat{U}_D(z)\exp[sz/(2D)]dz = 0. \tag{64}$$

Letting $D = D_n$ and $n \to \infty$ in (64), we get $R_* = m_u\gamma_u/(r_u - m_u)$ since $\hat{U}_D \to 1$ as $D \to \infty$. This completes the proof. $\square$

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REFERENCES

[1] M. G. Crandall and P. H. Rabinowitz, Bifurcation from simple eigenvalues, *J. Functional Analysis*, **8** (1971), 321–340.

[2] M. G. Crandall and P. H. Rabinowitz, Bifurcation, perturbation of simple eigenvalues and linearized stability, *Arch. Rational Mech. Anal.*, **52** (1973), 161–180.

[3] Y. Du and S. B. Hsu, Concentration phenomena in a nonlocal quasi-linear problem modeling phytoplankton I: Existence, *SIAM J. Math. Anal.*, **40** (2008), 1419–1440.

[4] Y. Du and S. B. Hsu, Concentration phenomena in a nonlocal quasi-linear problem modeling phytoplankton II: Limiting profile, *SIAM J. Math. Anal.*, **40** (2008), 1441–1470.

[5] Y. Du and S. B. Hsu, On a nonlocal reaction-diffusion problem arising from the modeling of phytoplankton growth, *SIAM J. Math. Anal.*, **42** (2010), 1305–1333.

[6] Y. Du and L. F. Mei, On a nonlocal reaction-diffusion-advection equation modelling phytoplankton dynamics, *Nonlinearity*, **24** (2011), 319–349.

[7] Y. Du, S. B. Hsu and Y. Lou, Multiple steady-states in phytoplankton population induced by photoinhibition, *J. Differential Equations*, **258** (2015), 2408–2434.

[8] M. Genkai-Kato, Y. Vadeboncoeur, L. Liboriussen and E. Jeppesen, Benthic-planktonic coupling, regime shifts, and whole-lake primary production in shallow lakes, *Ecology*, **93** (2012), 619–631.

[9] S. B. Hsu and Y. Lou, Single phytoplankton species growth with light and advection in a water column, *SIAM J. Appl. Math.*, **70** (2010), 2942–2974.

[10] S. B. Hsu, F. B. Wang and X. Q. Zhao, Global dynamics of zooplankton and harmful algae in flowing habitats, *J. Differential Equations*, **255** (2013), 265–297.

[11] J. Huisman, P. van Oostveen and F. J. Weissing, Species dynamics in phytoplankton blooms: incomplete mixing and competition for light, *Am. Nat.*, **154** (1999), 46–68.

[12] J. Huisman, N. N. P. Thi, D. M. Karl and B. Sommeijer, Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum, *Nature*, **439** (2006), 322–325.

[13] C. G. Jäger, S. Diehl and M. Emans, Physical determinants of phytoplankton production, algal stoichiometry, and vertical nutrient fluxes, *Am. Nat.*, **175** (2010), 91–104.

[14] C. G. Jäger and S. Diehl, Resource competition across habitat boundaries: asymmetric interactions between benthic and pelagic producers, *Ecol. Monogr.*, **84** (2014), 287–302.

[15] C. A. Klausmeier and E. Litchman, Algal games: The vertical distribution of phytoplankton in poorly mixed water columns, *Limnol. Oceanogr.*, **46** (2001), 1998–2007.

[16] T. Kolokolnikov, C. H. Ou and Y. Yuan, Phytoplankton depth profiles and their transitions near the critical sinking velocity, *J. Math. Biol.*, **59** (2009), 105–122.

[17] L. F. Mei and X. Y. Zhang, On a nonlocal reaction-diffusion-advection system modeling phytoplankton growth with light and nutrients, *Discrete Cont. Dyn. Syst.-B*, **17** (2012), 221–243.

[18] L. F. Mei and X. Y. Zhang, Existence and nonexistence of positive steady states in multi-species phytoplankton dynamics, *J. Differential Equations*, **253** (2012), 2025–2063.

[19] L. F. Mei, S. B. Hsu and F. B. Wang, Growth of single phytoplankton species with internal storage in a water column, *Discrete Cont. Dyn. Syst.-B*, **21** (2016), 607–620.

[20] H. Nie, S. B. Hsu and J. H. Wu, Coexistence solutions of a competition model with two species in a water column, *Discrete Cont. Dyn. Syst.-B*, **20** (2015), 2691–2714.

[21] R. Peng and X. Q. Zhao, A nonlocal and periodic reaction-diffusion-advection model of a single phytoplankton species, *J. Math. Biol.*, **72** (2016), 755–791.

[22] M. Scheffer, S. Szabó, A. Gragnani, E. H. van Nes, S. Rinaldi, N. Kautsky, J. Norberg, R. M. M. Roijackers and R. J. M. Franken, Floating plant dominance as a stable state, *Proc. Natl. Acad. Sci. USA*, **100** (2003), 4040–4045.

[23] J. P. Shi and X. F. Wang, On global bifurcation for quasilinear for quasilinear elliptic systems on bounded domains, *J. Differential Equations*, **246** (2009), 2788–2812.

[24] F. R. Vasconcelos, S. Diehl, P. Rodríguez, P. Hedström, J. Karlsson and P. Byström, Asymmetrical competition between aquatic primary producers in a warmer and browner world, *Ecology*, **97** (2016), 2580–2592.

[25] Y. Vadeboncoeur, G. Peterson, M. Vander Zanden and J. Kalff, Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light, *Ecology*, **89** (2008), 2542–2552.

[26] F. B. Wang, S. B. Hsu and X. Q. Zhao, A reaction-diffusion-advection model of harmful algae growth with toxin degradation, *J. Differential Equations*, **259** (2015), 3178–3201.

[27] F. B. Wang, A PDE system modeling the competition and inhibition of harmful algae with seasonal variations, *Nonlinear Analysis RWA*, **25** (2015), 258–275.

[28] X. F. Wang, Qualitative behavior of solutions of chemotactic diffusion systems: effects of motility and chemotaxis and dynamics, *SIAM J. Math. Anal.*, **31** (2000), 535–560.

[29] X. F. Wang and Q. Xu, Spiky and transition layer steady states of chemotaxis systems via global bifurcation and Helly's compactness theorem, *J. Math. Biol.*, **66** (2013), 1241–1266.

[30] K. Yoshiyama, J. P. Mellard, E. Litchman and C. A. Klausmeier, Phytoplankton competition for nutrients and light in a stratified water column, *Am. Nat.*, **174** (2009), 190–203.

[31] A. Zagaris, A. Doelman, N. N. Pham Thi and B. P. Sommeijer, Blooming in a nonlocal, coupled phytoplankton-nutrient model, *SIAM J. Appl. Math.*, **69** (2009), 1174–1204.

[32] A. Zagaris and A. Doelman, Emergence of steady and oscillatory localized structures in a phytoplankton-nutrient model, *Nonlinearity*, **24** (2011), 3437–3486.

[33] J. M. Zhang, J. P. Shi and X. Y. Chang, A mathematical model of algae growth in a pelagic-benthic coupled shallow aquatic ecosystem, *J. Math. Biol.*, **76** (2018), 1159–1193.

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