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A mathematical model of algae growth in a pelagic–benthic coupled shallow aquatic ecosystem

Jimin Zhang[1] · **Junping Shi**[2] · **Xiaoyuan Chang**[3]

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Abstract A coupled system of ordinary differential equations and partial differential equations is proposed to describe the interaction of pelagic algae, benthic algae and one essential nutrient in an oligotrophic shallow aquatic ecosystem with ample supply of light. The existence and uniqueness of non-negative steady states are completely determined for all possible parameter range, and these results characterize sharp threshold conditions for the regime shift from extinction to coexistence of pelagic and benthic algae. The influence of environmental parameters on algal biomass density is also considered, which is an important indicator of algal blooms. Our studies suggest that the nutrient recycling from loss of algal biomass may be an important factor in the algal blooms process; and the presence of benthic algae may limit the pelagic algal biomass density as they consume common resources even if the sediment nutrient level is high.

Keywords Reaction–diffusion model · Pelagic algae · Benthic algae · Nutrients · Environmental parameters · Algal biomass density

Mathematics Subject Classification 35J25 · 92D25 · 35A01

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✉ Junping Shi
jxshix@wm.edu

[1] School of Mathematical Sciences, Heilongjiang University, Harbin, Heilongjiang 150080, People's Republic of China

[2] Department of Mathematics, College of William and Mary, Williamsburg, VA 23187-8795, USA

[3] School of Applied Sciences, Harbin University of Science and Technology, Harbin, Heilongjiang 150080, People's Republic of China

1 Introduction

Algae are important primary producers of organic compounds through photosynthesis and chemosynthesis, and they form the base of the food chain in the lakes, oceans and other aquatic ecosystems. The growth of algae depends on light intensity, temperature and nutrients in the water, thus the vertical distribution of algae in the water column usually has a stratified structure. Especially, in shallow lakes or littoral zones, there are two distinct layers of algae: pelagic algae and benthic algae (Jäger and Diehl 2014; Scheffer et al. 2003; Vasconcelos et al. 2016).

Pelagic algae, typically phytoplankton, drift in the water column of lakes and oceans and provide significant biomass to aquatic ecosystems. It has been recognized that the growth of pelagic algae needs two essential resources: light and nutrients. The interaction between pelagic algae and its resources has been studied extensively in three possible ways, in both the theory and the real practical applications. One extreme case is in oligotrophic aquatic ecosystems with ample supply of light such that pelagic algae tend to compete only for nutrients (see Hsu et al. 2013; Mei et al. 2016; Nie et al. 2016, 2015; Wang et al. 2015); and the other extreme case is in eutrophic ecosystems with ample nutrient supply such that pelagic algae tend to compete only for light (see Du and Hsu 2010; Du and Mei 2011; Du et al. 2015; Hsu and Lou 2010; Huisman et al. 1999; Kolokolnikov et al. 2009; Mei and Zhang 2012a; Peng and Zhao 2016). In some aquatic ecosystems, pelagic algae compete for light and nutrients simultaneously (see Du and Hsu 2008a, b; Huisman et al. 2006; Jäger et al. 2010; Kerimoglu et al. 2012; Klausmeier and Litchman 2001; Ryabov et al. 2010; Yoshiyama et al. 2009; Zagaris et al. 2009; Zagaris and Doelman 2011).

Benthic algae (typically microalgae) are located in the bottom of lakes or oceans, and they attach to the surface of other plants and rocks or root in the sediment. There is growing evidence to show that benthic algae in some shallow, oligotrophic, clear-water ecosystem not only is an important food source of aquatic animals, but also influence water quality, energy cycle, and various biogeochemical interactions (Jäger and Diehl 2014; Scheffer et al. 2003; Vadeboncoeur et al. 2008). But there have been very few studies of the important role of benthic algae.

When both of pelagic and benthic algae are presented in an aquatic ecosystem, they may have an intense competition for light and nutrition. There have been existing dynamical models characterizing this relation between pelagic and benthic algae by using ordinary differential equations (see Jäger and Diehl 2014; Scheffer et al. 2003; Vasconcelos et al. 2016; Vadeboncoeur et al. 2008), in which an important assumption is that the pelagic habitat is well mixed to produce homogeneous vertical distributions of pelagic algae and nutrients in shallow water columns. However there is increasing recognition that the distributions of pelagic algae show strong spatial heterogeneity, both vertically and horizontally (see Du and Hsu 2008a, b; Huisman et al. 2002, 2006; Jäger et al. 2010; Klausmeier and Litchman 2001; Yoshiyama et al. 2009). Therefore it is important and of great interest to explore the effect of spatial heterogeneity on the pelagic and benthic algae growth, which has been neglected in previous studies, and establish some threshold conditions that cause a regime shift between coexistence and extinction of pelagic algae and benthic algae.

Motivated by the existing studies and the above considerations, in this study, we establish a coupled system of ordinary differential equations and partial differential equations to describe the interactions of pelagic algae, benthic algae and one essential nutrient in an oligotrophic shallow aquatic ecosystem with ample supply of light. The new model reveals the effect of the spatial heterogeneity of pelagic algae and gives threshold conditions of coexistence or regime shifts between pelagic algae and benthic algae. In addition, from the perspective of preventing algae blooms, we explore the influence of environmental parameters on algal biomass density. The present paper only focuses on the case where pelagic algae and benthic algae compete for an essential nutrient, while other possible cases (compete for light or for light and nutrients simultaneously) will be considered in forthcoming studies.

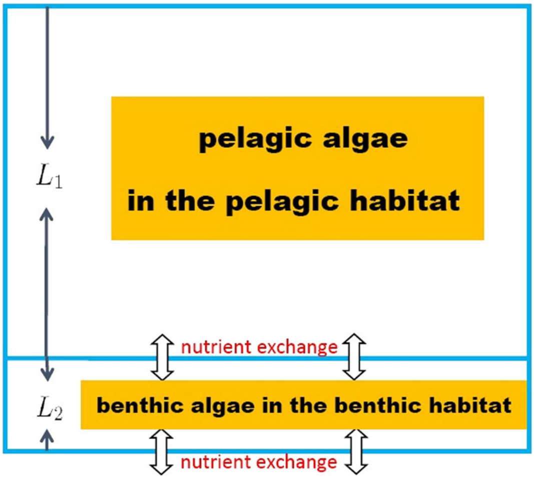
The rest of the paper is organized as follows. In Sect. 2, we derive a mathematical model of pelagic algae, benthic algae and nutrients consisting of two ordinary differential equations and two partial differential equations. In Sect. 3, we investigate dynamical properties of this model including the existence, uniqueness and stability of steady states, which are complemented by numerical simulations under reasonable parameter values from literature. In Sect. 4, we consider the influence of environmental parameters on algal biomass density via a systematic sensitivity analysis. In the discussion section, we summary our findings and state some biologically motivated mathematical questions for future study.

2 Model construction

In this section, we establish a mathematical model to describe the interactions between pelagic algae and benthic algae in an oligotrophic shallow aquatic ecosystem with ample supply of light, which means that pelagic algae and benthic algae tend to compete only for nutrients. We assume that the entire shallow aquatic area consists of two layers of habitat with uniform depth: pelagic habitat and benthic habitat. Let z denote the depth coordinate. We assume that $z = 0$ is the surface of the water, $z = L_3$ is the sediment surface (bottom of the lake/ocean), and $z = L_1 \in (0, L_3)$ is the interface between the pelagic and benthic habitats. Hence the positive z direction is from the surface of water to the bottom of lake/ocean. Here L_1 and $L_2 = L_3 - L_1$ are the thickness of pelagic habitat and benthic habitat respectively (see Fig. 1). In general, the benthic habitat closely contacts with the sediment and its thickness is far less than the depth of the pelagic habitat so $L_2 \ll L_1$. Therefore, here we assume that dissolved nutrients in the benthic habitat are well mixed and homogeneous in space.

A coupled system of two ordinary differential equations (ODE) and two partial differential equations (PDE) is established below to describe the dynamics of biomass density of pelagic algae (U), biomass density of benthic algae (V), concentration of dissolved nutrients in the pelagic habitat (R), concentration of dissolved nutrients in the benthic habitat (W). All the variables and parameters of the system and their biological significance are listed in Table 1.

Fig. 1 Interactions of pelagic algae, benthic algae and one essential nutrient in a shallow aquatic ecosystem



2.1 Pelagic algae and benthic algae

Let $U(z,t)$ denote the biomass density of pelagic algae at depth $z \in [0, L_1]$ and time t. The intrinsic growth rate of pelagic algae depends on the concentration of dissolved nutrients $R(z,t)$ in the pelagic habitat, and it takes a Michaelis–Menten type functional response form $r_u R/(R+\gamma_u)$, where r_u is the maximum production rate of pelagic algae, and γ_u is the half-saturation constant. On the other hand, the pelagic algal biomass density is lost at a density-independent rate m_u, caused by processes such as respiration, death and grazing. Pelagic algal transport is governed by passive movement due to turbulence with a depth independent turbulent diffusion coefficient D_u and also active movement due to sinking or buoyant with speed s. Taking together these assumptions results in the following reaction–diffusion–advection equation of U with no-flux boundary condition:

$$\begin{aligned}\frac{\partial U(z,t)}{\partial t} &= \text{turbulent diffusion} - \text{sinking(buoyant)} + \text{growth} - \text{loss}\\ &= D_u \frac{\partial^2 U}{\partial z^2} - s\frac{\partial U}{\partial z} + \left(\frac{r_u R}{R+\gamma_u} - m_u\right)U, \quad z \in (0, L_1),\\ D_u U_z(0) - sU(0) = 0,&\quad D_u U_z(L_1) - sU(L_1) = 0.\end{aligned} \tag{2.1}$$

The algae in the benthic habitat attach to the surface of other plants, rocks or roots in the sediment. This implies that they move very slowly or are motionless. Also the thickness of the benthic habitat is far less than the one of pelagic habitat, hence we assume that the density function V is spatially uniformly distributed. That is $V(z,t) \equiv V(t)$ for $z \in (L_1, L_3)$. The change in the benthic algal biomass density comes from two processes: growth and loss. The intrinsic growth rate of benthic algae is governed by the concentration of dissolved nutrients $W(z,t) \equiv W(t)$ in the benthic habitat, again with a Michaelis–Menten type functional response $r_v W/(W+\gamma_v)$, where r_v is the maximum production rate of the benthic algae, and γ_v is the half-saturation

Table 1 System variables and parameters with biological meanings and values

Symbol	Meaning	Value	Unit	Source
t	Time	–	Day	–
z	Depth	–	m	–
U	Biomass density of pelagic algae	–	$\mathrm{mgC/m^3}$	–
V	Biomass density of benthic algae	–	$\mathrm{mgC/m^3}$	–
R	Concentration of dissolved nutrients in the pelagic habitat	–	$\mathrm{mgP/m^3}$	–
W	Concentration of dissolved nutrients in the benthic habitat	–	$\mathrm{mgP/m^3}$	–
D_u	Vertical turbulent diffusivity of pelagic algae	2.59 (0.001–10)	$\mathrm{m^2/day}$	Huisman et al. (2002, 2006), Jäger et al. (2010), Kerimoglu et al. (2012), Klausmeier and Litchman (2001), Ryabov et al. (2010)
D_r	Vertical turbulent diffusivity of dissolved nutrients in the pelagic habitat	2.59 (0.001–10)	$\mathrm{m^2/day}$	Huisman et al. (2002, 2006), Jäger et al. (2010), Kerimoglu et al. (2012), Klausmeier and Litchman (2001), Ryabov et al. (2010)
s	Sinking or buoyant velocity of pelagic algae	0.05 (−5–5)	m/day	Huisman et al. (2002, 2006), Jäger et al. (2010), Jäger and Diehl (2014), Kerimoglu et al. (2012), Klausmeier and Litchman (2001), Ryabov et al. (2010), Vasconcelos et al. (2016)
r_u	Maximum specific production rate of pelagic algae	1	Day^{-1}	Huisman et al. (2002, 2006), Jäger and Diehl (2014), Ryabov et al. (2010)
r_v	Maximum specific production rate of benthic algae	1	Day^{-1}	Jäger and Diehl (2014)
m_u, m_v	Loss rate of pelagic and benthic algae, respectively	0.1	Day^{-1}	Jäger and Diehl (2014), Vasconcelos et al. (2016)
γ_u	Half saturation constant for nutrient-limited production of pelagic algae	3	$\mathrm{mgP/m^3}$	Jäger and Diehl (2014), Vasconcelos et al. (2016)

Table 1 continued

Symbol	Meaning	Value	Unit	Source
γ_v	Half saturation constant for nutrient-limited production of benthic algae	5	mgP/m^3	Jäger and Diehl (2014), Vasconcelos et al. (2016)
c_u	Phosphorus to carbon quota of pelagic algae	0.008	mgP/mgC	Vasconcelos et al. (2016)
c_v	Phosphorus to carbon quota of benthic algae	0.015	mgP/mgC	Vasconcelos et al. (2016)
a	Nutrient exchange rate between sediment and benthic habitat	0.05	m/day	Jäger and Diehl (2014), Vasconcelos et al. (2016)
b	Nutrient exchange rate between sediment and benthic habitat	0.05	m/day	Jäger and Diehl (2014), Vasconcelos et al. (2016)
L_1	Depth of the pelagic habitat (below water surface)	2	m	Jäger and Diehl (2014)
L_2	Vertical extent of the benthic habitat	0.01	m	Jäger and Diehl (2014), Vasconcelos et al. (2016)
W_{sed}	Concentration of dissolved nutrients in the sediment	10 (0.03–50)	mgP/m^3	Jäger and Diehl (2014), Vasconcelos et al. (2016)
β_u	Nutrient recycling proportion from loss of pelagic algal biomass	0.5 (0–1)	–	Jäger and Diehl (2014), Kerimoglu et al. (2012), Klausmeier and Litchman (2001), Ryabov et al. (2010), Vasconcelos et al. (2016)
β_v	Nutrient recycling proportion from loss of benthic algal biomass	0.3 (0–0.9)	–	Vasconcelos et al. (2016)

constant. The loss rate of benthic algal biomass density is scaled by a parameter m_v. Combining these assumptions give the following ODE for benthic algae:

$$\frac{dV(t)}{dt} = \text{growth} - \text{loss} = \left(\frac{r_v W}{W + \gamma_v} - m_v\right) V. \tag{2.2}$$

2.2 Nutrients in the pelagic and benthic habitats

The function $R(z, t)$ describes the concentration of dissolved nutrients in the pelagic habitat at depth $z \in [0, L_1]$ and time t, and $W(t)$ is the concentration of dissolved nutrients in the benthic habitat at time t. Here again due to the slow movement in the benthic habitat, the nutrient concentration in the benthic habitat is spatially uniform. The nutrients in the whole shallow aquatic ecosystems are supplied from the sediment with a fixed concentration W_{sed} there. The change of dissolved nutrients in the pelagic habitat depends on turbulent diffusion with a diffusion coefficient D_r, consumption by pelagic algae, recycling from the loss of pelagic algal biomass with carbon ratio c_u and proportion $\beta_u \in [0, 1]$, and nutrients exchange between the pelagic and benthic habitat at $z = L_1$ with nutrient exchange rate a. The dynamics of $R(z, t)$ is given by

$$\begin{aligned}\frac{\partial R(z,t)}{\partial t} &= \text{turbulent diffusion} + \text{recycling} - \text{consumption}\\ &= D_r \frac{\partial^2 R}{\partial z^2} + c_u \beta_u m_u U - \frac{c_u r_u R U}{R + \gamma_u}, \quad z \in (0, L_1),\\ R_z(0,t) = 0,\ &D_r R_z(L_1, t) = a(W(t) - R(L_1, t)) \text{ (nutrients exchange).}\end{aligned} \tag{2.3}$$

The benthic nutrient $W(t)$ could change as a result of consumption by benthic algae, recycling from the loss of benthic algal biomass with carbon ratios c_v and proportion $\beta_v \in [0, 1]$, nutrients exchange between the pelagic and benthic habitat, and supplying from the sediment. Thus the dynamics of $W(t)$ is described as

$$\begin{aligned}\frac{dW(t)}{dt} &= \text{supplying} - \text{nutrients exchange} + \text{recycling} - \text{consumption}\\ &= \frac{b}{L_2}(W_{sed} - W) - \frac{a}{L_2}(W - R(L_1, t)) + c_v \beta_v m_v V - \frac{c_v r_v W V}{W + \gamma_v}.\end{aligned} \tag{2.4}$$

In Eqs. (2.3) and (2.4), we include the recycle of nutrients $c_u \beta_u m_u U$ and $c_v \beta_v m_v V$. This is because high temperature can cause the rapid decomposition of algae, and thus promote more nutritious to be recycled. In previous studies, there are very few dynamical results on recycling. Here our subsequent studies show that the nutrient recycling from loss of algal biomass may be an important factor in the existence and uniqueness of non-negative steady state solutions and the algal blooms process.

Also in (2.1) and (2.2), we do not include the exchange of algaes between pelagic habit and benthic habit, as the experiments in Jäger et al. (2010), Scheffer et al. (2003), Vasconcelos et al. (2016) show that there is no algal exchange between the pelagic and benthic habitat found in these situations.

2.3 The full model

Combining all Eqs. (2.1)–(2.4), we have the following full system of pelagic algae-benthic algae-nutrients model:

$$\begin{cases} \dfrac{\partial U}{\partial t} = D_u \dfrac{\partial^2 U}{\partial z^2} - s\dfrac{\partial U}{\partial z} + \dfrac{r_u RU}{R+\gamma_u} - m_u U, & 0 < z < L_1,\ t > 0, \\ \dfrac{dV}{dt} = \dfrac{r_v WV}{W+\gamma_v} - m_v V, & t > 0, \\ \dfrac{\partial R}{\partial t} = D_r \dfrac{\partial^2 R}{\partial z^2} + c_u \beta_u m_u U - \dfrac{c_u r_u RU}{R+\gamma_u}, & 0 < z < L_1,\ t > 0, \\ \dfrac{dW}{dt} = \dfrac{b}{L_2}(W_{sed} - W) - \dfrac{a}{L_2}(W - R(L_1,t)) + c_v \beta_v m_v V - \dfrac{c_v r_v WV}{W+\gamma_v}, & t > 0, \\ D_u \dfrac{\partial U}{\partial z}(0,t) - sU(0,t) = 0,\ D_u \dfrac{\partial U}{\partial z}(L_1,t) - sU(L_1,t) = 0, & t > 0, \\ \dfrac{\partial R}{\partial z}(0,t) = 0,\ D_r \dfrac{\partial R}{\partial z}(L_1,t) = a(W(t) - R(L_1,t)), & t > 0. \end{cases} \tag{2.5}$$

In consideration of the biological significance of (2.5), we assume that $s \in \mathbb{R}$, $\beta_u, \beta_v \in [0, 1]$ and the remaining parameters are all positive constants. Furthermore, we consider the solutions of (2.5) with nonnegative initial values, *i.e.*

$$\begin{aligned} &U(z,0) = U_0(z) \geq\not\equiv 0, \quad R(z,0) = R_0(z) \geq\not\equiv 0, \quad 0 \leq z \leq L_1, \\ &V(0) = V_0 \geq 0, \quad W(0) = W_0 \geq 0. \end{aligned} \tag{2.6}$$

In the following we study the dynamics of (2.5). In particular, we are interested in the existence, uniqueness, and stability of non-negative steady state solutions $(U(z), V, R(z), W)$ which satisfy the following steady state system:

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

3 Existence and stability of steady states

The main purpose of this section is to investigate the existence, uniqueness and local/global stability of non-negative steady state solutions of (2.5). The possible non-negative steady states of (2.5) are listed below:

1. Nutrient-only semi-trivial steady state $E_1 : (0, 0, R_1(z), W_1)$, where $(R_1(z), W_1)$ solves

$$\begin{cases} R''(z) = 0,\ 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) = 0, \\ R'(0) = 0,\ D_r R'(L_1) = a(W - R(L_1)); \end{cases} \tag{3.1}$$

2. Benthic algae-nutrient semi-trivial steady state $E_2 : (0, V_2, R_2(z), W_2)$, where $(V_2, R_2(z), W_2)$ solves

$$\begin{cases} \dfrac{r_v W}{W+\gamma_v} - m_v = 0, \\ R''(z) = 0, \ 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) + c_v L_2 \left(\beta_v m_v - \dfrac{r_v W}{W+\gamma_v} \right) V = 0, \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)); \end{cases} \tag{3.2}$$

3. Pelagic algae-nutrient semi-trivial steady state $E_3 : (U_3(z), 0, R_3(z), W_3)$, where $(U_3(z), R_3(z), W_3)$ solves

$$\begin{cases} D_u U''(z) - sU'(z) + \left(\dfrac{r_u R(z)}{R(z)+\gamma_u} - m_u \right) U(z) = 0, & 0 < z < L_1, \\ D_r R''(z) + c_u \beta_u m_u U(z) - \dfrac{c_u r_u R(z) U(z)}{R(z)+\gamma_u} = 0, & 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) = 0, & \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, & \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)); & \end{cases} \tag{3.3}$$

4. Coexistence steady state $E_4 : (U_4(z), V_4, R_4(z), W_4)$, where $(U_4(z), V_4, R_4(z), W_4)$ solves

$$\begin{cases} D_u U''(z) - sU'(z) + \left(\dfrac{r_u R(z)}{R(z)+\gamma_u} - m_u \right) U(z) = 0, & 0 < z < L_1, \\ \dfrac{r_v W}{W+\gamma_v} - m_v = 0, & \\ D_r R''(z) + c_u \beta_u m_u U(z) - \dfrac{c_u r_u R(z) U(z)}{R(z)+\gamma_u} = 0, & 0 < z < L_1, \\ b(W_{sed} - W) - a(W - R(L_1)) + c_v L_2 \left(\beta_v m_v - \dfrac{r_v W}{W+\gamma_v} \right) V = 0, & \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, & \\ R'(0) = 0, D_r R'(L_1) = a(W - R(L_1)). & \end{cases} \tag{3.4}$$

In the following subsections, we will discuss the existence, uniqueness and local stability of steady states in each form categorized above, and also discuss the implication of such steady states to the whole dynamics of (2.5).

To establish the local stability of the above steady states, we linearize the system (2.5) about a steady state $(\bar{u}(z), \bar{v}, \bar{r}(z), \bar{w})$ and obtain an eigenvalue problem

$$\begin{cases} \lambda\varphi(z) = D_u \varphi''(z) - s\varphi'(z) + \left(\dfrac{r_u \bar{r}(z)}{\bar{r}(z)+\gamma_u} - m_u \right) \varphi(z) + \dfrac{r_u \gamma_u \bar{u}(z)}{(\bar{r}(z)+\gamma_u)^2} \phi(z), & 0 < z < L_1, \\ \lambda\xi = \left(\dfrac{r_v \bar{w}}{\bar{w}+\gamma_v} - m_v \right) \xi + \dfrac{r_v \gamma_v \bar{v}}{(\bar{w}+\gamma_v)^2} \zeta, & \\ \lambda\phi(z) = \left(c_u \beta_u m_u - \dfrac{c_u r_u \bar{r}(z)}{\bar{r}(z)+\gamma_u} \right) \varphi(z) + D_r \phi''(z) - \dfrac{c_u r_u \gamma_u \bar{u}(z)}{(\bar{r}(z)+\gamma_u)^2} \phi(z), & 0 < z < L_1, \\ \lambda\zeta = \left(c_v \beta_v m_v - \dfrac{c_v r_v \bar{w}}{\bar{w}+\gamma_v} \right) \xi - \dfrac{c_v r_v \gamma_v \bar{v}}{(\bar{w}+\gamma_v)^2} \zeta + \dfrac{a}{L_2} \phi(L_1) - \left(\dfrac{a+b}{L_2} \right) \zeta, & \\ D_u \varphi' - s\varphi|_{z=0,L_1} = 0, \ \phi'(0) = 0, \ D_r \phi'(L_1) = a(\zeta - \phi(L_1)). & \end{cases} \tag{3.5}$$

A steady state solution of (2.5) is locally asymptotically stable if all eigenvalues of (3.5) have negative real part, and it is unstable if at least one eigenvalue has positive real part. Note that here for (2.5), the linear stability defined by (3.5) (consisting of reaction–diffusion equations and ordinary differential equations) implies the nonlinear local stability (uniformly asymptotically stable) in some proper function spaces (see Henry 1981, Chapter 5). Similar stability of steady state solutions of shadow systems of reaction–diffusion systems have been considered in Ni et al. (2001a, b).

Before we discuss each possible steady state as introduced above, we notice the following observation for the dynamics of the system (2.5).

Proposition 3.1 *Let* $(U(z,t), V(t), R(z,t), W(t))$ *be a solution of* (2.5) *with initial condition specified as in* (2.6).

1. *If* $m_u > r_u$, *then* $\lim_{t\to\infty} U(x,t) = 0$ *uniformly for* $x \in [0, L_1]$*;*
2. *If* $m_v > r_v$, *then* $\lim_{t\to\infty} V(t) = 0$.

Proof From the equation of $V(t)$, we have $V'(t) \le (r_v - m_v)V(t)$, thus it is clear that if $m_v > r_v$, then $\lim_{t\to\infty} V(t) = 0$. On the other hand, from

$$\frac{\partial U}{\partial t} \le D_u \frac{\partial^2 U}{\partial z^2} - s\frac{\partial U}{\partial z} + (r_u - m_u)U,$$

and $m_u > r_u$, we obtain that $u(x,t)$ converges to 0 uniformly for $x \in [0, L_1]$ as $t \to \infty$ by the comparison theorem of parabolic equations. □

The result in Proposition 3.1 indicates that when $m_u > r_u$, the dynamics of (2.5) is effectively reduced to benthic algae-nutrients subsystem, while when $m_v > r_v$, the dynamics of (2.5) is effectively reduced to pelagic algae-nutrients subsystem.

3.1 Nutrient-only semi-trivial steady state

For any parameter value, there is a unique nutrient-only steady state that is in balance with the sediment nutrient concentration W_{sed}, and it is at least locally asymptotically stable when the algae's loss rates are high.

Theorem 3.2 *The system* (2.5) *has a unique nutrient-only steady state solution*

$$E_1 \equiv (0, 0, W_{sed}, W_{sed}). \tag{3.6}$$

Moreover if

$$m_u > \frac{r_u W_{sed}}{W_{sed} + \gamma_u} \quad \text{and} \quad m_v > \frac{r_v W_{sed}}{W_{sed} + \gamma_v}, \tag{3.7}$$

then E_1 *is locally asymptotically stable with respect to* (2.5), *and if*

$$0 < m_u < \frac{r_u W_{sed}}{W_{sed} + \gamma_u} \quad \text{or} \quad 0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}, \tag{3.8}$$

then E_1 *is unstable.*

Proof It is easy to see that E_1 given in (3.6) is the unique solution of (3.1). For the stability of $E_1(0, 0, W_{sed}, W_{sed})$, it follows from (3.5) that the stability of E_1 is determined by the eigenvalue problem

$$\lambda\varphi(z) = D_u\varphi''(z) - s\varphi'(z) + \left(\frac{r_u W_{sed}}{W_{sed}+\gamma_u} - m_u\right)\varphi(z),\ 0 < z < L_1, \tag{3.9a}$$

$$\lambda\xi = \left(\frac{r_v W_{sed}}{W_{sed}+\gamma_v} - m_v\right)\xi, \tag{3.9b}$$

$$\lambda\phi(z) = \left(c_u\beta_u m_u - \frac{c_u r_u W_{sed}}{W_{sed}+\gamma_u}\right)\varphi(z) + D_r\phi''(z),\ 0 < z < L_1, \tag{3.9c}$$

$$\lambda\zeta = \left(c_v\beta_v m_v - \frac{c_v r_v W_{sed}}{W_{sed}+\gamma_v}\right)\xi + \frac{a}{L_2}\phi(L_1) - \left(\frac{a+b}{L_2}\right)\zeta, \tag{3.9d}$$

$$D_u\varphi' - s\varphi|_{z=0,L_1} = 0,\ \phi'(0) = 0,\ D_r\phi'(L_1) = a(\zeta - \phi(L_1)). \tag{3.9e}$$

To establish the local stability of E_1, we set

$$h_1 = \frac{r_u W_{sed}}{W_{sed}+\gamma_u} - m_u,\ h_2 = \frac{r_v W_{sed}}{W_{sed}+\gamma_v} - m_v.$$

Let λ_1 be the largest eigenvalue of (3.9), and let $(\varphi, \xi, \phi, \zeta)$ be the corresponding eigenfunction. We consider the following three cases: (a_1) $\varphi \not\equiv 0$; (a_2) $\varphi = 0$ and $\xi \neq 0$; or (a_3) $\varphi = 0$ and $\xi = 0$.
Case (a_1): $\varphi \not\equiv 0$. In this case, the stability of E_1 is completely described by characteristic equations (3.9a), (3.9c), (3.9d). Let $\varphi = e^{(s/D_u)z}\tilde{\varphi}$. Then (3.9a) translates into

$$\begin{cases} \lambda\tilde{\varphi}(z) = D_u\tilde{\varphi}''(z) + s\tilde{\varphi}'(z) + h_1\tilde{\varphi}(z), \quad 0 < z < L_1, \\ \tilde{\varphi}'(0) = \tilde{\varphi}'(L_1) = 0. \end{cases} \tag{3.10}$$

It is easy to see that the dominant eigenvalue of (3.10) is h_1 and the corresponding eigenfunction is $\tilde{\varphi}_1(z) = 1$. Then the dominant eigenvalue of (3.9a) is $\lambda_1 = h_1$ and the corresponding eigenfunction is $\varphi(z) = e^{sz/D_u}$. Substituting λ_1 and $\varphi(z)$ into (3.9c) and (3.9d) we have

$$\zeta = \frac{a}{a+b+h_1L_2}\phi(L_1), \tag{3.11a}$$

$$\phi(z) = -\frac{c_u(m_u(1-\beta_u)+h_1)e^{sz/D_u}}{h_1} + \frac{D_r\phi''(z)}{h_1},\ 0 < z < L_1, \tag{3.11b}$$

$$\phi'(0) = 0,\ D_r\phi'(L_1) = -\frac{a(b+h_1L_2)}{a+b+h_1L_2}\phi(L_1). \tag{3.11c}$$

Solving (3.11b) one has that

$$\phi_1(z) = \hat{c}_1 e^{z\sqrt{h_1/D_r}} + \hat{c}_2 e^{-z\sqrt{h_1/D_r}} + \frac{c_u D_u^2(m_u(1-\beta_u)+h_1)e^{sz/D_u}}{s^2D_r - h_1D_u^2},\ \hat{c}_1, \hat{c}_2 \in \mathbb{R},$$

when $\sqrt{h_1/D_r} \neq s/D_u$, or

$$\phi_1(z) = \hat{c}_3 e^{z\sqrt{h_1/D_r}} + \hat{c}_4 e^{-z\sqrt{h_1/D_r}} + \frac{c_u D_u(m_u(1-\beta_u)+h_1)ze^{sz/D_u}}{2sD_r}, \ \hat{c}_3, \hat{c}_4 \in \mathbb{R},$$

when $\sqrt{h_1/D_r} = s/D_u$. It follows from the boundary conditions (3.11c) that there exist constants $\hat{c}_i$ $(i = 1, 2, 3, 4)$ such that $\phi_1(z)$ satisfies (3.11c). This shows that there exists a solution $(\zeta, \phi(z))$ satisfying Eq. (3.11). Therefore, in case (a_1), $\lambda_1 = h_1$ determines the stability of E_1.

Case (a_2): $\varphi = 0$ and $\xi \not\equiv 0$. In this case it follows from (3.9b) that $\lambda_1 = h_2$ with eigenfunction $\xi = 1$. Combining (3.9c) with (3.9d), we have

$$\begin{cases} \zeta = \dfrac{a}{a+b+h_2L_2}\phi(L_1) - \dfrac{c_vL_2(h_2+m_v(1-\beta_v))}{a+b+h_2L_2}, \\ \phi(z) = \dfrac{D_r\phi''(z)}{h_2}, \ 0 < z < L_1, \\ \phi'(0) = 0, \ D_r\phi'(L_1) = -a\left[\dfrac{b+h_2L_2}{a+b+h_1L_2}\phi(L_1) + \dfrac{c_vL_2(h_2+m_v(1-\beta_v))}{a+b+h_1L_2}\right]. \end{cases} \tag{3.12}$$

It is straightforward to show that there exists a solution $(\zeta, \phi(z))$ satisfying Eq. (3.12). This implies that $\lambda_1 = h_2$ determines the stability of E_1 in case (a_2).

Case (a_3): $\varphi = 0$ and $\xi = 0$. Now (3.9) reduces to

$$\begin{cases} \lambda\phi(z) = D_r\phi''(z), \ 0 < z < L_1, \\ \lambda\zeta = \dfrac{a\phi(L_1)}{L_2} - \dfrac{(a+b)\zeta}{L_2}, \\ \phi'(0) = 0, \ D_r\phi'(L_1) = a(\zeta - \phi(L_1)). \end{cases} \tag{3.13}$$

If $\zeta = 0$ in (3.13), then ϕ satisfies

$$\lambda\phi(z) = D_r\phi''(z), \ 0 < z < L_1, \ \phi'(0) = 0, \ \phi'(L_1) = 0, \ \phi(L_1) = 0, \tag{3.14}$$

which implies that $\phi(z) = 0$. Hence $\zeta \neq 0$, and consequently $\phi(z) \not\equiv 0$ and (ϕ, ζ) satisfies

$$\begin{cases} \zeta = \dfrac{a}{a+b+\lambda L_2}\phi(L_1), \\ \lambda\phi(z) = D_r\phi''(z), \ 0 < z < L_1, \\ \phi'(0) = 0, \ D_r\phi'(L_1) = -\dfrac{a(b+\lambda L_2)}{a+b+\lambda L_2}\phi(L_1). \end{cases} \tag{3.15}$$

If $\lambda > 0$ is an eigenvalue of (3.15), then from $\phi'(0) = 0$ we have $\phi(z) = \cosh(\omega z)$ for $\omega = \sqrt{\lambda/D_r}$. But from the boundary condition at $x = L_1$, we get

$$D_r \sinh(\omega L_1) = -\frac{a(b+\lambda L_2)}{a+b+\lambda L_2}\cos(\omega L_1),$$

that is a contradiction. It is also easy to see $\lambda = 0$ cannot be an eigenvalue of (3.15). Thus the eigenvalues of (3.15) must be negative. Indeed for $\lambda < 0$, we have $\phi(z) = \cos(\omega z)$ for $\omega = \sqrt{-\lambda/D_r}$ since $\phi'(0) = 0$. From the boundary condition at $x = L_1$, we find that

$$\tan(\omega L_1) = \frac{(a/D_r)(b - \omega^2 D_r L_2)}{\omega(a + b - \omega^2 D_r L_2)}. \tag{3.16}$$

Then the dominant eigenvalue λ_1 of (3.15) is $-D_r\omega_1^2$, where ω_1 is the smallest positive root of (3.16). Summarizing above discussions, we conclude that in case (a_3), λ_1 is negative.

In view of case (a_1)–(a_3), we conclude that $\lambda_1 = \max\{h_1, h_2, -D_r\omega_1^2\}$, and if (3.7) holds, then $\lambda_1 < 0$ and E_1 is locally asymptotically stable. On the other hand, if (3.8) holds, then E_1 is unstable. □

The condition (3.7) implies that large algal loss rates in both the pelagic and benthic habitats lead to extinction of both algae population. Indeed we prove next that the extinction is global for all initial conditions if a stronger condition on the loss rates is satisfied.

Theorem 3.3 *Suppose that*

$$m_u > r_u, \quad \textit{and} \quad m_v > r_v, \tag{3.17}$$

then the nutrient-only steady state solution $E_1 \equiv (0, 0, W_{sed}, W_{sed})$ *is globally asymptotically stable for* (2.5) *with respect to any nonnegative initial value.*

Proof From Proposition 3.1, we have $\lim_{t\to\infty} u(x, t) = 0$ uniformly for $x \in [0, L_1]$ and $\lim_{t\to\infty} V(t) = 0$ provided (3.17) holds. From the theory of asymptotical autonomous systems Mischaikow et al. (1995), (2.5) reduces to a limiting system

$$\begin{cases} \dfrac{\partial R}{\partial t} = D_r \dfrac{\partial^2 R}{\partial z^2}, & 0 < z < L_1,\ t > 0, \\ \dfrac{dW}{dt} = \dfrac{b}{L_2}(W_{sed} - W) - \dfrac{a}{L_2}(W - R(L_1, t)), & t > 0, \\ \dfrac{\partial R}{\partial z}(0, t) = 0,\ D_r \dfrac{\partial R}{\partial z}(L_1, t) = a(W(t) - R(L_1, t)), & t > 0. \end{cases} \tag{3.18}$$

In order to obtain our results, we construct a Lyapunov function for system (3.18):

$$V(R, W) = \frac{1}{2}\int_0^{L_1} (R(z) - W_{sed})^2 dz + \frac{L_2}{2}(W - W_{sed})^2.$$

Let $(R(z, t), W(t))$ be an arbitrary solution of (3.18) with nonnegative initial values. Then

$$\frac{dV(R(\cdot, t), W(t))}{dt} = \int_0^{L_1} (R(z, t) - W_{sed}) \frac{\partial R}{\partial t} dz + L_2(W(t) - W_{sed}) \frac{dW}{dt}$$

$$\begin{aligned}
&= \int_0^{L_1} (R(z,t) - W_{sed}) \frac{\partial^2 R}{\partial z^2} dz - b(W(t) - W_{sed})^2 \\
&\quad - a(W(t) - W_{sed})(W(t) - R(L_1,t)) \\
&= D_r \frac{\partial R}{\partial z}(R - W_{sed})\Big|_0^{L_1} - \int_0^{L_1} \left(\frac{\partial R}{\partial z}\right)^2 dz \\
&\quad - b(W(t) - W_{sed})^2 - a(W(t) - W_{sed})(W(t) - R(L_1,t)) \\
&= a(W(t) - R(L_1,t))(R(L_1,t) - W_{sed}) - \int_0^{L_1} \left(\frac{\partial R}{\partial z}\right)^2 dz \\
&\quad - b(W(t) - W_{sed})^2 - a(W(t) - W_{sed})(W(t) - R(L_1,t)) \\
&= -a(W(t) - R(L_1,t))^2 - b(W_{sed} - W(t))^2 - \int_0^{L_1} \left(\frac{\partial R}{\partial z}\right)^2 dz \le 0.
\end{aligned}$$

Note that $dV(\cdot)/dt = 0$ holds if and only if $W(t) = W_{sed}$, $R(L_1,t) = W(t)$, and $\partial R/\partial z = 0$, that is, $W(t) \equiv R(z,t) \equiv W_{sed}$. It follows from the LaSalle's Invariance Principle that $(R(z,t), W(t))$ converges to (W_{sed}, W_{sed}) uniformly for $x \in [0, L_1]$ as $t \to \infty$ for (3.18), and it also follows that any solution of (2.5) with nonnegative initial value converges to E_1 as $t \to \infty$. □

We remark that the global stability of (W_{sed}, W_{sed}) in the nutrient-only subspace always holds without the condition (3.17), as shown in the proof of Theorem 3.3. The global stability in Theorem 3.3 also implies that under the condition (3.17), there exist no any other steady state solutions such as E_2, E_3, E_4 as mentioned in the beginning of this section.

3.2 Benthic algae-nutrient semi-trivial steady state

In this subsection, we prove that when the benthic algal loss rate m_v is not large, then benthic algae is able to grow to a positive equilibrium level. In fact, we show that $m_v^* = r_v W_{sed}/(W_{sed} + \gamma_v)$ is a sharp threshold for the persistence/extinction of benthic algae.

Theorem 3.4 *The system* (2.5) *has a positive benthic algae-nutrient semi-trivial steady state* E_2 *if and only if*

$$0 \le \beta_v < 1, \quad m_u > 0, \quad 0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}. \tag{3.19}$$

Whenever E_2 *exists, it is unique and it is given by*

$$E_2 \equiv (0, V_2, R_2(z), W_2) = \left(0, \frac{b(W_{sed} - W_2)}{c_v m_v L_2(1-\beta_v)}, \frac{\gamma_v m_v}{r_v - m_v}, \frac{\gamma_v m_v}{r_v - m_v}\right). \tag{3.20}$$

Moreover if in addition to (3.19)*, we also have*

$$m_u > \frac{r_u \gamma_v m_v}{\gamma_v m_v + \gamma_u (r_v - m_v)}, \tag{3.21}$$

then E_2 is locally asymptotically stable with respect to (2.5)*, while E_2 is unstable if*

$$0 < m_u < \frac{r_u \gamma_v m_v}{\gamma_v m_v + \gamma_u (r_v - m_v)}. \tag{3.22}$$

Proof The steady state equation (3.2) can be explicitly solved. The equation of R and its boundary conditions imply that $W_2 = R_2$. The value of W_2 can be solved from the first equation of (3.2), and finally V_2 can be solved from the third equation of (3.2). Thus E_2 must be given by (3.20). And it is easy to verify that (V_2, R_2, W_2) is positive if and only if (3.19) holds.

Next we investigate the stability of E_2. From (3.5), the stability of E_2 is determined by the eigenvalue problem

$$\lambda\varphi(z) = D_u\varphi''(z) - s\varphi'(z) + h_3\varphi(z),\ 0 < z < L_1, \tag{3.23a}$$

$$\lambda\xi = \frac{r_v\gamma_v V_2}{(W_2+\gamma_v)^2}\zeta, \tag{3.23b}$$

$$\lambda\phi(z) = -[c_u(m_u(1-\beta_u)+h_3)]\varphi(z) + D_r\phi''(z),\ 0 < z < L_1, \tag{3.23c}$$

$$\lambda\zeta = c_v m_v(\beta_v - 1)\xi - \frac{c_v r_v\gamma_v V_2}{(W_2+\gamma_v)^2}\zeta + \frac{a}{L_2}\phi(L_1) - \left(\frac{a+b}{L_2}\right)\zeta, \tag{3.23d}$$

$$D_u\varphi' - s\varphi|_{z=0,L_1} = 0,\ \phi'(0) = 0,\ D_r\phi'(L_1) = a(\zeta - \phi(L_1)), \tag{3.23e}$$

where

$$h_3 = \frac{r_u W_2}{W_2 + \gamma_u} - m_u.$$

Again let λ_1 be the largest eigenvalue of (3.23), and let $(\varphi, \xi, \phi, \zeta)$ be the corresponding eigenfunction. We consider two cases: (b_1): $\varphi \not\equiv 0$, or (b_2): $\varphi \equiv 0$.

Case (b_1): $\varphi \not\equiv 0$. Carrying out similar arguments as those of case (a_1) in Theorem 3.2, we conclude that the dominant eigenvalue of (3.23a) is $\lambda_1 = h_3$ and the corresponding eigenfunction is $\varphi(z) = e^{sz/D_u}$. With this λ_1 and $\varphi(z)$, $(\xi, \phi(z), \zeta)$ in (3.23) can be uniquely solved.

Case (b_2): $\varphi = 0$. If $\xi = 0$, then it is clear that $\zeta = 0$ as well. Then (3.23) reduces into (3.14) again, thus the dominant eigenvalue is $\lambda_1 = -(D_r\pi^2)/L_1^2$ and the corresponding eigenfunction is $\phi(z) = \cos(\pi z/L_1)$. If $\xi \neq 0$, then (3.23) is reformulated as

$$\begin{cases} \lambda\xi = h_4\zeta, \\ \lambda\phi(z) = D_r\phi''(z),\ 0 < z < L_1, \\ \lambda\zeta = \dfrac{c_v m_v h_4(\beta_v - 1)\zeta}{\lambda} - c_v h_4\zeta + \dfrac{a}{L_2}\phi(L_1) - \left(\dfrac{a+b}{L_2}\right)\zeta, \\ \phi'(0) = 0,\ D_r\phi'(L_1) = -\dfrac{a(L_2\lambda^2 + (b + c_v h_4 L_2)\lambda + c_v m_v h_4 L_2(1-\beta_v))}{a(L_2\lambda^2 + (a + b + c_v h_4 L_2)\lambda + c_v m_v h_4 L_2(1-\beta_v))}\phi(L_1), \end{cases} \tag{3.24}$$

where $h_4 = r_v \gamma_v V_2/(W_2 + \gamma_v)^2$. Then similar to case (a_3) in Theorem 3.2, (3.24) has only negative eigenvalues, and the dominant eigenvalue $\lambda_1 = -D_r \eta_1^2$, where η_1 is the smallest root of

$$\tan \eta L_1 = \frac{a[D_r L_2 \eta^4 - (b + c_v h_4 L_2) D_r \eta^2 + c_v m_v h_4 L_2 (1 - \beta_v)]}{D_r \eta [D_r L_2 \eta^4 - (a + b + c_v h_4 L_2) D_r \eta^2 + c_v m_v h_4 L_2 (1 - \beta_v)]}.$$

Combining the cases (b_1) and (b_2), we conclude that E_2 is locally asymptotically stable if $h_3 < 0$ which is equivalent to (3.21), and E_2 is unstable if $h_3 > 0$ which is equivalent to (3.22). □

Remark 3.5 1. It follows from (3.20) that V_2 increases with respect to the recycling proportion β_v and $\lim_{\beta_v \to 1^-} V_2 = \infty$. This implies that the benthic algae-nutrient semi-trivial steady state E_2 does not exist when $\beta_v = 1$. From the perspective of ecological point of view, if the recycling proportion β_v from the loss of benthic algal biomass is high, then there is a benthic algal bloom in this oligotrophic shallow aquatic ecosystem with ample supply of light.

2. One can see that $\lim_{m_v \to m_v^*} E_2 = E_1$, where $m_v^* = r_v W_{sed}/(W_{sed} + \gamma_v)$. Hence $m_v = m_v^*$ is a critical value for the existence/nonexistence of benthic algae-nutrient steady state E_2.
3. If $m_u > r_u$, then from Proposition 3.1, one has that $\lim_{t \to \infty} U(x, t) = 0$. Thus the pelagic algae become extinct in this case, and the system (2.5) reduces to the subsystem of benthic algae and (pelagic and benthic) nutrients. It is an interesting question whether E_2 is globally asymptotically stable in this situation, which is indicated by our numerical simulations.

3.3 Pelagic algae-nutrient semi-trivial steady state

In the oligotrophic shallow aquatic ecosystem, it is also possible that pelagic algae can grow while benthic algae become extinct. In this subsection, we show the existence and uniqueness of pelagic algae-nutrients semi-trivial steady state, in which benthic algae is absent in the system. Such a steady state is in a form of $E_3 = (U_3, 0, R_3, W_3)$ with (U_3, R_3, W_3) being a positive solution of (3.3).

We first establish some *a priori* estimates for positive solutions of (3.3).

Lemma 3.6 *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* (3.3) *and* $\beta_u \in [0, 1)$. *Then*

(i) $0 < m_u < \dfrac{r_u W_{sed}}{W_{sed} + \gamma_u}$;

(ii) R_3 *is a strictly increasing function on* $[0, L_1]$ *and* $\dfrac{\beta_u \gamma_u m_u}{r_u - \beta_u m_u} \le R_3(z) < W_{sed}$ *for all* $z \in [0, L_1]$;

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

(iv) $U_3(z) e^{-sz/D_u}$ *is a strictly increasing function of* z *on* $(0, L_1)$, *and for any* $\varepsilon > 0$, *there exists a positive constant* $A(\varepsilon)$ *such that* $\|U_3\|_\infty \le A(\varepsilon)$ *if* $m_u \in [\varepsilon, r_u W_{sed}/(W_{sed} + \gamma_u))$.

Proof (i): It follows from the first equation of (3.3) and its boundary conditions that

$$\begin{cases} -D_u U_3''(z) + sU_3'(z) - \left(\dfrac{r_u R_3(z)}{R_3(z)+\gamma_u}\right) U_3(z) = -m_u U_3(z), \ 0 < z < L_1, \\ D_u U_3'(0) - sU_3(0) = D_u U_3'(L_1) - sU_3(L_1) = 0. \end{cases} \tag{3.25}$$

Hence the principal eigenvalue of (3.25) is

$$\lambda_1 \left(-\frac{r_u R_3(\cdot)}{R_3(\cdot)+\gamma_u}\right) = -m_u,$$

with principal eigenfunction U_3. From the monotonicity of the principal eigenvalue on the weight functions, we have

$$-\frac{r_u W_{sed}}{W_{sed}+\gamma_u} = \lambda_1\left(-\frac{r_u W_{sed}}{W_{sed}+\gamma_u}\right) < \lambda_1\left(-\frac{r_u R_3(\cdot)}{R_3(\cdot)+\gamma_u}\right) < \lambda_1(0) = 0.$$

This means that $0 < m_u < r_u W_{sed}/(W_{sed}+\gamma_u)$.

(ii) and (iii): It follows from the first two equations of (3.3) and its boundary conditions that

$$\begin{aligned} &\int_0^{L_1} \left(\frac{r_u R_3(z)}{R_3(z)+\gamma_u} - m_u\right) U_3(z)dz = 0, \\ &a(W_3 - R_3(L_1)) + c_u \int_0^{L_1} \left(\beta_u m_u - \frac{r_u R_3(z)}{R_3(z)+\gamma_u}\right) U_3(z)dz = 0. \end{aligned} \tag{3.26}$$

Since $\beta_u \in [0, 1)$, we have $R_3(L_1) < W_3$. From the third equation of (3.3), we have

$$W_3 = \frac{aR_3(L_1) + bW_{sed}}{a+b} < W_{sed}. \tag{3.27}$$

This proves (iii) as $W_3 > 0$. It follows from (3.27) that $R_3(z)$ satisfies

$$\begin{cases} D_r R_3''(z) + c_u \left(\beta_u m_u - \dfrac{r_u R_3(z)}{R_3(z)+\gamma_u}\right) U_3(z) = 0, \ 0 < z < L_1, \\ R_3'(0) = 0, \ D_r R_3'(L_1) = \dfrac{ab(W_{sed} - R_3(L_1))}{a+b} > 0. \end{cases} \tag{3.28}$$

To prove the upper bound of $R_3(z)$, we set

$$\begin{aligned} \Omega_1 &:= \{z \in [0, L_1] : \beta_u m_u \le r_u R_3(z)/(R_3(z)+\gamma_u), \ z \in \Omega_1\}, \\ \Omega_2 &:= \{z \in [0, L_1] : \beta_u m_u > r_u R_3(z)/(R_3(z)+\gamma_u), \ z \in \Omega_2\}. \end{aligned}$$

It is clear that

$$\Omega_1 \cap \Omega_2 = \emptyset,\ \Omega_1 \cup \Omega_2 = [0, L_1],\ \ \inf_{z\in\Omega_1} R_3(z)|_{\Omega_1} \geq \sup_{z\in\Omega_2} R_3(z)|_{\Omega_2}.$$

We show that $\Omega_2 = \emptyset$. We consider the following two cases: (c_1) $0 \in \Omega_1$; (c_2) $0 \in \Omega_2$. Case (c_1): $0 \in \Omega_1$. For any $z \in \Omega_1$, $R_3''(z) \geq 0$ and $R_3'(z)$ is increasing for z on Ω_1. This shows that $R_3'(z) \geq 0$ for all $z \in \Omega_1$ and $R_3(z)$ is an increasing function of z on Ω_1 since $R_3'(0) = 0$ holds. Note that $\inf_{z\in\Omega_1} R_3(z)|_{\Omega_1} \geq \sup_{z\in\Omega_2} R_3(z)|_{\Omega_2}$ and $R_3(z)$ is continuous, then $x \in \Omega_1$ for any $x \in (0, L_1]$ and $\Omega_2 = \emptyset$;
Case (c_2): $0 \in \Omega_2$. For any $z \in \Omega_2$, $R_3''(z) < 0$ and $R_3'(z)$ is a strictly decreasing function of z on Ω_2. It follows from $0 \in \Omega_2$ that $R_3(z)$ is strictly decreasing for z on Ω_2, then $x \in \Omega_2$ for any $x \in (0, L_1]$. But on the other hand $L_1 \in \Omega_1$ since $R_3'(L_1) > 0$. This is a contradiction. Therefore, $0 \notin \Omega_2$.

Combining cases (c_1) and (c_2), we conclude that $R_3(z)$ is strictly increasing for $z \in [0, L_1]$ as $R_3'(L_1) > 0$. By the boundary conditions of (3.28) and the definition of Ω_1, we have $R_3(0) \geq \beta_u\gamma_u m_u/(r_u - \beta_u m_u)$ and $R_3(L_1) < W_{sed}$, which implies that (ii) holds.

(iv): It follows from the first equality of (3.26) and $U_3 > 0$ that $r_u R_3/(R_3 + \gamma_u) - m_u$ must change sign in $(0, L_1)$. From the monotonicity of R_3, we conclude that $r_u R_3(z)/(R_3(z) + \gamma_u) - m_u$ is an increasing function of z on $(0, L_1)$. This means that there is a $z^* \in (0, L_1)$ such that $r_u R_3(z)/(R_3(z) + \gamma_u) - m_u < 0$ for $z \in (0, z^*)$ and $r_u R_3(z)/(R_3(z)+\gamma_u) - m_u > 0$ for $z \in (z^*, L_1)$. Combining the first equation of (3.3) with its boundary conditions, we have $D_u U_3'(z) - sU_3(z) > 0$ for any $z \in (0, L_1)$. Then $U_3(z)e^{-sz/D_u}$ is a strictly increasing function of z on $(0, L_1)$.

To establish the boundedness of $U_3(z)$, for any $\varepsilon > 0$, we assume that there are a sequence $m_u^i \in [\varepsilon, r_u W_{sed}/(W_{sed} + \gamma_u)]$ and corresponding positive solutions $(U_3^i(z), R_3^i(z), W_3^i)$ of (3.3) such that $\|U_3^i\|_\infty \to \infty$ as $i \to \infty$. Without loss of generality, we assume that $m_u^i \to \bar{m}_u$ as $i \to \infty$. Let $u_i = U_3^i/\|U_3^i\|_\infty$. Then u_i satisfies

$$\begin{cases} -(D_u u_i'(z) - su_i(z))' + m_u^i u_i(z) = \left(\dfrac{r_u R_3^i(z)}{R_3^i(z) + \gamma_u}\right) u_i(z),\ 0 < z < L_1, \\ D_u u_i'(0) - su_i(0) = D_u u_i'(L_1) - su_i(L_1) = 0, \\ \displaystyle\int_0^{L_1} \left(\frac{r_u R_3^i(z)}{R_3^i(z) + \gamma_u} - m_u^i\right) u_i(z)dz = 0. \end{cases}$$

It follows from (ii) that $0 < r_u R_3^i(z)/(R_3^i(z) + \gamma_u) < r_u W_{sed}/(W_{sed} + \gamma_u)$ for all $z \in [0, L_1]$, which means that we may assume that there is a function $d_1 \in C([0, L_1])$ such that $r_u R_3^i(z)/(R_3^i(z) + \gamma_u) \to d_1(z)$ in $C([0, L_1])$ as $i \to \infty$. Noting that $\{u_i\}$, $\{m_u^i\}$ are both bounded in $L^\infty[0, L_1]$, by using L^p theory for elliptic operators and the Sobolev embedding theorem, we may assume (passing to a subsequence if necessary) that $u_i \to u$ in $C^1([0, L_1])$ as $i \to \infty$, and u satisfies (in the weak sense)

$$\begin{cases} -(D_u u'(z) - su(z))' + \bar{m}_u u(z) = d_1(z)u(z), \ 0 < z < L_1, \\ D_u u'(0) - su(0) = D_u u'(L_1) - su(L_1) = 0, \\ \displaystyle\int_0^{L_1} (d_1(z) - \bar{m}_u)u(z)dz = 0. \end{cases} \tag{3.29}$$

Since $u \geq 0$ and $\|u\|_\infty = 1$, it follows from the strong maximum principle that $u > 0$ on $[0, L_1]$. On the other hand, R_3^i satisfies

$$\begin{cases} D_r(R_3^i(z))'' = c_u \left(\dfrac{r_u R_3^i(z)}{R_3^i(z) + \gamma_u} - \beta_u m_u^i \right) u_i(z) \|U_3^i\|_\infty, \ 0 < z < L_1, \\ (R_3^i)'(0) = 0, \ D_r(R_3^i)'(L_1) = \dfrac{ab(W_{sed} - R_3^i(L_1))}{a+b}. \end{cases} \tag{3.30}$$

Choosing $d_2 \in C^\infty([0, L_1])$ with $d_2'|_{z=0,L_1} = 0$ and $d_2 > 0$ on $[0, L_1]$, and multiplying both sides of (3.30) by d_2 and integrating in $(0, L_1)$, we have

$$\begin{aligned} &\left(\frac{ab}{a+b}\right) d_2(L_1)(W_{sed} - R_3^i(L_1)) + \int_0^{L_1} R_3^i(z)(d_2(z))''dz \\ &\quad = c_u \|U_3^i\|_\infty \int_0^{L_1} \left(\frac{r_u R_3^i(z)}{R_3^i(z) + \gamma_u} - \beta_u m_u^i \right) u_i(z)dz. \end{aligned}$$

Dividing by $\|U_3^i\|_\infty$ on both sides of the above equality and letting $i \to \infty$ give

$$0 = \int_0^{L_1} (d_1(z) - \beta_u \bar{m}_u)u(z)dz = \int_0^{L_1} (1 - \beta_u)\bar{m}_u u(z)dz,$$

since the third equation of (3.29) holds. This is a contradiction to $\beta_u \in [0, 1)$, $\bar{m}_u \in [\varepsilon, r_u W_{sed}/(W_{sed} + \gamma_u)]$ and $u > 0$ on $[0, L_1]$. Hence the boundedness of U_3 holds for $m_u \in [\varepsilon, r_u W_{sed}/(W_{sed} + \gamma_u))$. □

It is noteworthy that if $(U_3, R_3, W_3) \in C([0, L_1]) \times C([0, L_1]) \times \mathbb{R}_+$ is a nonnegative solution of (3.3) with $U_3 \not\equiv 0$, then (U_3, R_3, W_3) is a positive solution of (3.3). In fact, we first claim that $U_3(0) > 0$ and $R_3(0) > 0$. Suppose that $U_3(0) = 0$, then $U_3'(0) = 0$ from the boundary condition of U_3, so $U_3(z) \equiv 0$ for $z \in [0, L_1]$ from (3.25). Hence we have $U_3(0) > 0$. Next we assume that $R_3(0) = 0$. From (3.28), we have $D_r R_3''(0) = -c_u \beta_u m_u U_3(0) < 0$. Since $R_3(0) = R_3'(0) = 0$, then $R_3(z) < 0$ for $z \in (0, \delta)$ for some $\delta > 0$, that is a contradiction to $R_3(z) \geq 0$ for all $z \in [0, L_1]$. Therefore we must have $R_3(0) > 0$. By using the maximum principle, we get $R_3(z) > 0$ for all $z \in [0, L_1]$. On the other hand, similarly, we have $U_3(0) > 0$, $U_3(1) > 0$ and

$$\begin{cases} -D_u U_3''(z) + sU_3'(z) + m_u U_3(z) = \dfrac{r_u R_3(z)U_3(z)}{R_3(z) + \gamma_u} \geq\not\equiv 0, \ 0 < z < L_1, \\ D_u U_3'(0) - sU_3(0) = D_u U_3'(L_1) - sU_3(L_1) = 0, \end{cases}$$

which imply that $U_3(z) > 0$ for all $z \in [0, L_1]$ from the strong maximum principle.

It follows from (3.27), (3.28) and (3.25) that (3.3) is equivalent to

$$W = \frac{aR(L_1) + bW_{sed}}{a+b} \le W_{sed}$$

and $(U(z), R(z))$ satisfies

$$\begin{cases} D_u U''(z) - sU'(z) + \left(\dfrac{r_u R(z)}{R(z)+\gamma_u} - m_u\right) U(z) = 0, & 0 < z < L_1, \\ D_r R''(z) + c_u \left(\beta_u m_u - \dfrac{r_u R(z)}{R(z)+\gamma_u}\right) U(z) = 0, & 0 < z < L_1, \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, \\ R'(0) = 0,\ D_r R'(L_1) = \dfrac{ab(W_{sed} - R(L_1))}{a+b} \ge 0. \end{cases} \tag{3.31}$$

Hence the existence and uniqueness of positive solutions of (3.3) is reduced to the existence and uniqueness of positive solutions of (3.31). Note that (3.31) is an elliptic system with predator-prey type nonlinearity. We recall the following assertion for the non-degeneracy of positive solutions of such system.

Lemma 3.7 *If* (U_3, R_3) *is a positive solution of* (3.31)*, then the linearization of* (3.31) *with respect to* (U_3, R_3)*, which is given by*

$$\begin{cases} D_u \varphi''(z) - s\varphi'(z) + \left(\dfrac{r_u R_3(z)}{R_3(z)+\gamma_u} - m_u\right) \varphi(z) + \dfrac{r_u \gamma_u U_3(z)}{(R_3(z)+\gamma_u)^2}\phi(z) = 0, & 0 < z < L_1, \\ \left(c_u \beta_u m_u - \dfrac{c_u r_u R_3(z)}{R_3(z)+\gamma_u}\right) \varphi(z) + D_r \phi''(z) - \dfrac{c_u r_u \gamma_u U_3(z)}{(R_3(z)+\gamma_u)^2}\phi(z) = 0, & 0 < z < L_1, \\ D_u \varphi' - s\varphi|_{z=0,L_1} = 0,\ \phi'(0) = 0,\ D_r \phi'(L_1) + \dfrac{ab}{a+b}\phi(L_1) = 0, \end{cases}$$

only has the trivial solution. This means that (U_3, R_3) *is non-degenerate.*

The proof of Lemma 3.7 is similar to that of Nie et al. (2015, Lemma 3.1) and López-Gómez and Pardo (1993, Lemma 3.1), so we omit it here.

We now embed our problem into the framework of topological degree theory. We first assume that $m_u \in [\varepsilon, r_u W_{sed}/(W_{sed} + \gamma_u))$, $\beta_u \in [0, 1)$ hold for some $\varepsilon > 0$ and let $\omega(z) = W_{sed} - R(z)$ for any $z \in [0, L_1]$ and $0 < R(z) < W_{sed}$. Then there is a positive constant K_1 such that

$$\frac{W_{sed} - \omega(z)}{W_{sed} - \omega(z) + \gamma_u} \ge \frac{W_{sed}}{W_{sed} + \gamma_u} - K_1 \omega(z).$$

Let

$$X := \{(\mu, \nu) \in C([0, L_1]) \times C([0, L_1]) : \mu \ge 0,\ \nu \ge 0\},$$
$$\Omega := \{(\mu, \nu) \in X : \mu < A + 1,\ \nu < W_{sed} + 1\}.$$

Then X is the positive cone in $C([0, L_1]) \times C([0, L_1])$ and Ω is a bounded open subset of X. For any $(U, \omega) \in \Omega$, we consider

$$\begin{cases} -(D_u\varphi''(z) - s\varphi'(z)) + K_2\varphi(z) = \left(\dfrac{\kappa r_u(W_{sed} - \omega(z))}{(W_{sed} - \omega(z)) + \gamma_u} - m_u\right) U(z) + K_2U(z), & 0 < z < L_1, \\ -D_r\phi''(z) + K_2\phi(z) = \left(\dfrac{c_u r_u(W_{sed} - \omega(z))}{(W_{sed} - \omega(z)) + \gamma_u} - c_u\beta_u m_u\right) U(z) + K_2\omega(z), & 0 < z < L_1, \\ D_u\varphi' - s\varphi|_{z=0,L_1} = 0, \ \phi'(0) = 0, \ D_r\phi'(L_1) + \dfrac{ab}{a+b}\phi(L_1) = 0, \end{cases} \tag{3.32}$$

where $\kappa \in [0, 1]$ and K_2 is large enough such that

$$K_2 > \max\left\{m_u - \frac{\kappa r_u(W_{sed} - \omega(z))}{(W_{sed} - \omega(z)) + \gamma_u}, c_u r_u K_1 \omega U\right\}.$$

Denote the solution operator $(\varphi, \phi) = T_\kappa(U, \omega)$ for any $(U, \omega) \in \Omega$. It follows from the strong maximum principle and standard elliptic regularity theory that $T_\kappa : \Omega \to X$, compact and continuously differentiable for any $\kappa \in [0, 1]$. Moreover, (3.31) has a nonnegative solution if and only if the operator T_1 has a fixed point in Ω. Carrying out similar arguments as Theorem 3.4 in Nie et al. (2015), we have the following conclusions:

(e_1) index$(T_1, \Omega, X) = 1$ and index$(T_1, (0, 0), X) = 0$;
(e_2) if $(\hat{U}, \hat{R})$ is a positive solution of (3.31) and non-degenerate, then index$(T_1, (\hat{U}, \hat{\omega}), X) = 1$, where $\hat{\omega} = 1 - \hat{R}$.

It follows from the compactness of T_1 and the non-degeneracy of its fixed points (see Lemma 3.7) that the operator T_1 has at most finitely many positive fixed points in Ω, denoted as $(\hat{U}_i, \hat{\omega}_i)$, $i = 1, 2, \ldots, N$. From (e_1) and (e_2), we have

$$N = \text{index}(T_1, (0, 0), X) + \sum_{i=1}^{N} \text{index}(T_1, (\hat{U}_i, \hat{\omega}_i), X) = \text{index}(T_1, \Omega, X) = 1,$$

which implies that (3.31) has a unique positive solution. Therefore, we obtain the following conclusion.

Theorem 3.8 *The system* (2.5) *has a pelagic algae-nutrient semi-trivial steady state* E_3 *if and only if*

$$0 \le \beta_u < 1, \quad 0 < m_u < \frac{r_u W_{sed}}{W_{sed} + \gamma_u}, \quad m_v > 0, \tag{3.33}$$

and whenever E_3 *exists, it is unique and non-degenerate.*

Remark 3.9 1. It follows from a standard bifurcation argument [see Du and Hsu (2008a), Mei and Zhang 2012b] that when $m_u \to 0$, $\|U_3^{m_u}\|_\infty \to \infty$. This indicates the occurrence of a pelagic algal bloom, which is a serious environmental problem.

2. If $m_v > r_v$, then from Proposition 3.1, one has that $\lim_{t\to\infty} V(t) = 0$. Thus the benthic algae become extinct in this case, and the system (2.5) reduces to the subsystem of pelagic algae and (pelagic and benthic) nutrients.
3. Although the pelagic algae-nutrients semi-trivial steady state E_3 is unique and non-degenerate, its stability is not known (just as other diffusive predator-prey systems). But for realistic environmental parameters, our numerical simulation shows that under (3.33), solutions of (2.5) converge to E_3.
4. In case of ample supply of light, recycling of nutrients does not alter the monotony of nutrition with water depth (see (ii) in Lemma 3.6), but it has an important impact on the existence and uniqueness of pelagic algae-nutrient semi-trivial steady state E_3 (for $\beta_u \in [0, 1)$ and for $\beta_u = 1$) and pelagic algal biomass (see Sect. 4).

3.4 Coexistence steady state

A coexistence steady state solution of (2.5) is the one whose each component is positive. The result in Proposition 3.1 shows that a coexistence steady state can only exist when $0 < m_u \le r_u$ and $0 < m_v \le r_v$. A direct calculation gives

$$W_4 = \frac{\gamma_v m_v}{r_v - m_v},\ \ V_4 = \frac{b(W_{sed} - W_4) + a(W_4 - R_4(L_1))}{c_v m_v L_2(1-\beta_v)} \tag{3.34}$$

since the second and fourth equations of (3.4) hold. Similar to (3.26), we conclude that $R_4(L_1) \le W_4$, and the equal sign holds if and only if $\beta_u = 1$. It is clear that if V_4 is positive, then

$$0 \le \beta_v < 1,\ 0 < m_v < \frac{r_v W_{sed}}{\gamma_v + W_{sed}}.$$

It follows from (3.34) that the existence and uniqueness of positive solutions of (3.4) is equivalent to the existence and uniqueness of positive solutions of the following system

$$\begin{cases} D_u U''(z) - sU'(z) + \left(\dfrac{r_u R(z)}{R(z)+\gamma_u} - m_u\right) U(z) = 0, & 0 < z < L_1, \\ D_r R''(z) + c_u\left(\beta_u m_u - \dfrac{r_u R(z)}{R(z)+\gamma_u}\right) U(z) = 0, & 0 < z < L_1, \\ D_u U'(0) - sU(0) = D_u U'(L_1) - sU(L_1) = 0, & \\ R'(0) = 0,\ D_r R'(L_1) = a\left(\dfrac{\gamma_v m_v}{r_v - m_v} - R(L_1)\right) \ge 0. & \end{cases} \tag{3.35}$$

We now state our main results in this subsection.

Lemma 3.10 *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* (3.4) *and* $\beta_u \in [0, 1)$. *Then*

(v) $0 \le \beta_v < 1,\ 0 < m_u < \dfrac{r_u \gamma_v m_v}{\gamma_v m_v + \gamma_u(r_v - m_v)}$ *and* $0 < m_v < \dfrac{r_v W_{sed}}{W_{sed} + \gamma_v}$;

(vi) *$R_4(z)$ is a strictly increasing function on $[0, L_1]$ and* $\dfrac{\beta_u\gamma_u m_u}{r_u - \beta_u m_u} \le R_4(z) < \dfrac{\gamma_v m_v}{r_v - m_v}$ *for all $z \in [0, L_1]$;*

(vii) *$U_4(z)e^{-sz/D_u}$ is a strictly increasing function of z on $(0, L_1)$, and for any $\varepsilon > 0$, there exists a positive constant $B(\varepsilon)$ such that $\|U_4\|_\infty \le B(\varepsilon)$ if $m_u \in [\varepsilon, r_u\gamma_v m_v/(\gamma_v m_v + \gamma_u(r_v - m_v))$.*

Theorem 3.11 *The system (2.5) has a positive coexistence steady state E_4 if and only if*

$$0 \le \beta_u, \beta_v < 1, \quad 0 < m_u < \frac{r_u\gamma_v m_v}{\gamma_v m_v + \gamma_u(r_v - m_v)}, \quad 0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}, \tag{3.36}$$

and whenever E_4 exists, it is unique and non-degenerate.

The proofs of Lemma 3.10 and Theorem 3.11 are similar to those of Lemma 3.6 and Theorem 3.8 respectively, and here we omit them.

Remark 3.12 1. This existence and uniqueness of coexistence steady state under (3.36) shows that pelagic algae and benthic algae competing for one essential nutrient can coexist in the oligotrophic shallow aquatic ecosystem with ample supply of light.

2. A bifurcation approach can be used to show that the coexistence steady state E_4 bifurcates from the benthic algae-nutrient semi-trivial steady state E_2 at $m_u = \dfrac{r_u\gamma_v m_v}{\gamma_v m_v + \gamma_u(r_v - m_v)}$ when $0 < m_v < \dfrac{r_v W_{sed}}{W_{sed} + \gamma_v}$ is satisfied. Similarly the pelagic algae-nutrient semi-trivial steady state E_3 bifurcates from the nutrient-only semi-trivial steady state E_1 at $m_u = \dfrac{r_u W_{sed}}{W_{sed} + \gamma_u}$ for any $m_v > 0$. The bifurcation structure of E_i $(i = 1, 2, 3, 4)$ and associated exchange of stability will be considered in a forthcoming paper.
3. If the loss of pelagic and benthic algal biomass is completely recycled back to pelagic and benthic nutrients ($\beta_u = 1$ and $\beta_v = 1$), then coexistence steady state E_4 dose not exist.

3.5 Simulations of steady states

In this subsection, we show some numerical simulations to illustrate our analysis of steady states for model (2.5). In order to facilitate our simulations below, we partition the parameter ranges in Table 2 and summarize our main results on the existence, uniqueness and stability of steady state solutions shown in previous subsections.

Note that the parameter space of (m_u, m_v) is partitioned into the following regions according to Table 2 (see Fig. 2):

$$\Delta_1 := \left\{(m_u, m_v) : m_u > \frac{r_u W_{sed}}{W_{sed} + \gamma_u},\ m_v > \frac{r_v W_{sed}}{W_{sed} + \gamma_v}\right\},$$

$$\Delta_2 := \left\{(m_u, m_v) : m_u > \frac{r_u\gamma_v m_v}{\gamma_v m_v + \gamma_u(r_v - m_v)},\ 0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}\right\},$$

Table 2 Existence, uniqueness and stability of steady states for model (2.5)

Steady states	Existence and uniqueness	Local stability
$E_1 = (0, 0, R_1, W_1)$	Always	$m_u > \frac{r_u W_{sed}}{W_{sed} + \gamma_u}, m_v > \frac{r_v W_{sed}}{W_{sed} + \gamma_v}$
$E_2 = (0, V_2, R_2, W_2)$	$0 \le \beta_v < 1,\ 0 < m_u,$ $0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}$	$m_u > \frac{r_u \gamma_v m_v}{\gamma_v m_v + \gamma_u (r_v - m_v)}$
$E_3 = (U_3, 0, R_3, W_3)$	$0 \le \beta_u < 1,\ 0 < m_v,$ $0 < m_u < \frac{r_u W_{sed}}{W_{sed} + \gamma_u}$	Unknown
$E_4 = (U_4, V_4, R_4, W_4)$	$0 \le \beta_u, \beta_v < 1, 0 < m_u < \frac{r_u \gamma_v m_v}{\gamma_v m_v + \gamma_u (r_v - m_v)},$ $0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}$	Unknown

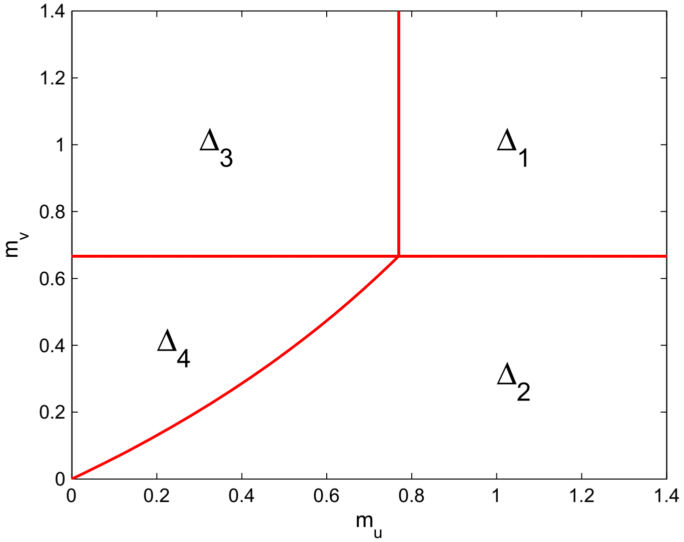


Fig. 2 The parameter ranges in the (m_u, m_v) plane with different extinction/existence scenarios, as defined in Table 2. Here the parameter values see Table 1

$$\Delta_3 := \left\{(m_u, m_v) : 0 < m_u < \frac{r_u W_{sed}}{W_{sed} + \gamma_u},\ m_v > \frac{r_v W_{sed}}{W_{sed} + \gamma_v}\right\},$$

$$\Delta_4 := \left\{(m_u, m_v) : 0 < m_u < \frac{r_u \gamma_v m_v}{\gamma_v m_v + \gamma_u (r_v - m_v)},\ 0 < m_v < \frac{r_v W_{sed}}{W_{sed} + \gamma_v}\right\}.$$

Figures 3, 4, 5, 6 show the simulations of solutions of (2.5) for different algal loss rates (m_u, m_v) while other parameters are realistic ones from Table 1, and in each

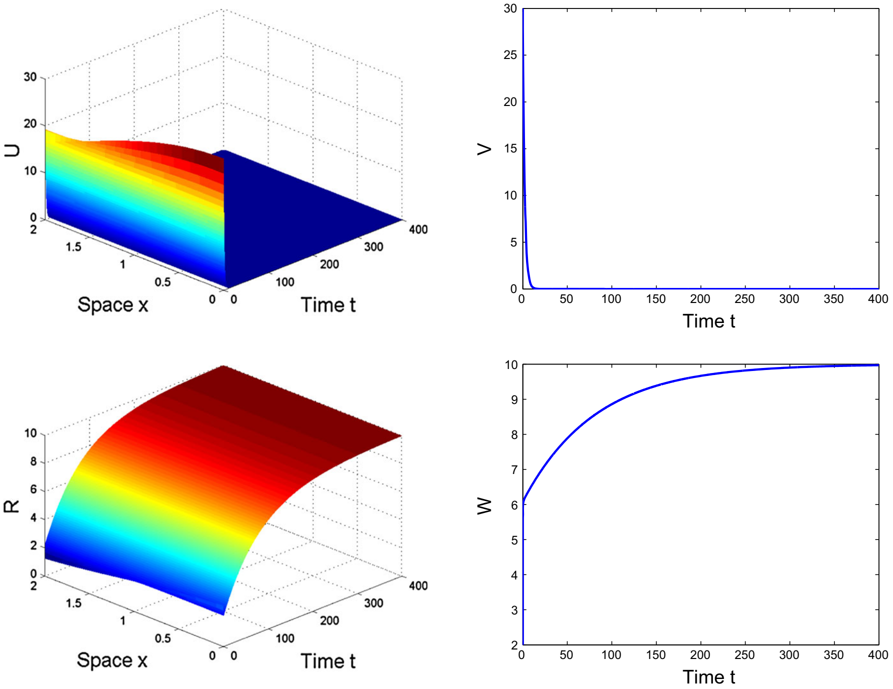


Fig. 3 Nutrient-only semi-trivial steady state E_1. Here $m_u = 1$, $m_v = 1$ and other parameters are from Table 1

case the solution converges to a steady state. The simulations appear to have same convergence results regardless of initial conditions.

For the case of $(m_u, m_v) = (1, 1)$, one can see that the extinction of both pelagic algae and benthic algae may arise from this model with the concentration of dissolved nutrients in the pelagic habitat and benthic habitat reaching the concentration of dissolved nutrients in the sediment (see Theorem 3.2, Δ_1 in Figs. 2, and 3). This means that in the absence of algae, dissolved nutrients is distributed evenly over the whole shallow aquatic area.

For $(m_u, m_v) = (1, 0.4)$, the pelagic algae becomes extinct and the benthic algae persists (see Theorem 3.4, Δ_2 in Figs. 2, and 4). In this case, the equilibrium nutrient levels in two habitats are still the same but are considerably lower than the sediment concentration. If $(m_u, m_v) = (0.2, 1)$, the benthic algae dies out and the pelagic algae reaches a high level (see Theorem 3.8, Δ_3 in Figs. 2, and 5). Also here the dissolved nutrient in pelagic habitat is much lower than the one in benthic habitat. The transition from Fig. 4 to Fig. 5 also indicates that there is a regime shift between pelagic algae and benthic algae, where the dominance of benthic algae transforms into the dominance of pelagic algae in a shallow aquatic ecosystem.

Finally for $(m_u, m_v) = (0.1, 0.4)$, both of pelagic and benthic algae in the habitat maintain a positive level (see Theorem 3.11, Δ_4 in Figs. 2, and 6). From Figs. 7 and 8, we can see that $(U_3(z), R_3(z))$ and $(U_4(z), R_4(z))$ are both nonconstant steady states. Indeed in both cases, the pelagic algae $U(z)$ and pelagic nutrient $R(z)$ appear to be

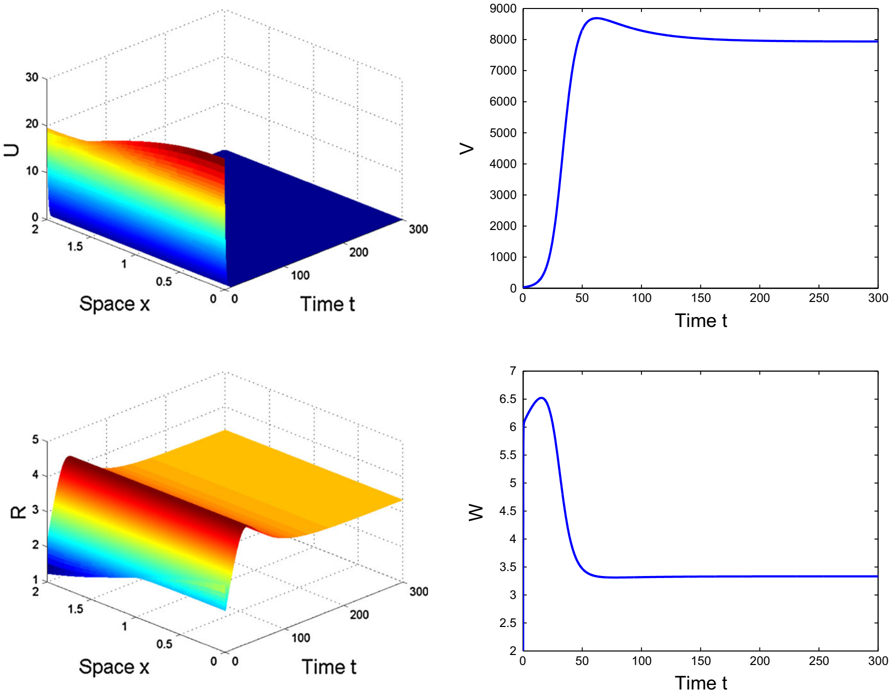


Fig. 4 Benthic algae-nutrient semi-trivial steady state E_2. Here $m_u = 1$, $m_v = 0.4$ and other parameters are from Table 1

increasing from the water surface $z = 0$ to the pelagic-benthic interface $z = L_1$, which verify the monotonicity results shown in Lemmas 3.6 and 3.10.

4 Influence of environmental parameters on algal biomass

The algal biomass density in an aquatic ecosystems is an important index for evaluating water quality and protecting biological diversity. Especially, algal blooms, exhibited by excessive proliferation of algae on account of the excessive amounts of nitrogen and phosphorus in the water, is a secondary pollution and may produce great harm to environment and human health. Therefore, in this section, we will explore the influence of model parameters in (2.5) on the pelagic algal biomass density and benthic algal biomass density. In order to facilitate the discussion below, we use the spatial average of $U(x, t)$ and $R(x, t)$ defined as

$$\overline{U}(t) = \frac{1}{L_1} \int_0^{L_1} U(t, z)dz, \ \overline{R}(t) = \frac{1}{L_1} \int_0^{L_1} R(t, z)dz.$$

In figures below, we compare the (spatial averaged) coexistence steady states $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for different parameter values.

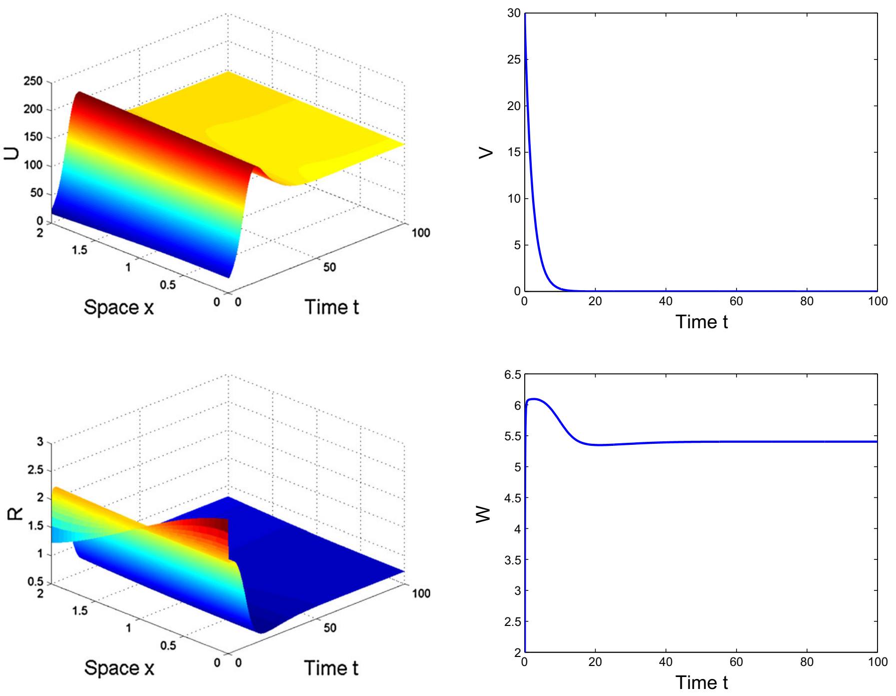


Fig. 5 Pelagic algae-nutrient semi-trivial steady state E_3. Here $m_u = 0.2$, $m_v = 1$ and other parameters are from Table 1

First we observe the effect of nutrient recycling proportion β_u and β_v from loss of algal biomass. The parameters β_u, β_v are closely related and proportional to the ambient temperature or light intensity. We assume that parameters (m_u, m_v) are chosen so that the coexistence steady state E_4 can be achieved, then we vary β_u and keep $\beta_v = 0$ to compare the biomass of E_4. From Fig. 9 left panel, one can observe that pelagic algal biomass mean density increases and benthic algal biomass density almost keeps unchanged with the increase of β_u. Note that in Theorem 3.11, the existence of E_4 is only shown when $\beta_u < 1$. When $\beta_u = 1$ (the loss of pelagic algal biomass is completely recycled back to pelagic nutrients), the pelagic algae biomass appears to be increasing indefinitely (see Fig. 9 right panel). This shows that algal blooms may still occur even in nutrient-poor aquatic ecosystems (here $W_{sed} = 10$), and it happens because rapid decomposition of dead algae in high temperature leads to adequate nutrient supply, which in turn causes algal blooms. The similar phenomenon also occurs for benthic algae when β_v increases to 1 (see Fig. 10). Indeed the expression of V_4 in (3.34) explicitly shows that $V_4 \to \infty$ as $\beta_v \to 1$. These indicate that the nutrient recycling from loss of algal biomass may be an important factor in the algal blooms process.

Our theoretical results in Section 3 have shown that the change of mortality rates m_u, m_v can cause the regime shift from one steady state to another. Here we observe the effect of m_u and m_v on the coexistence state algal biomass density. Comparing the changes in pelagic algal biomass mean density reveals that benthic algae could control

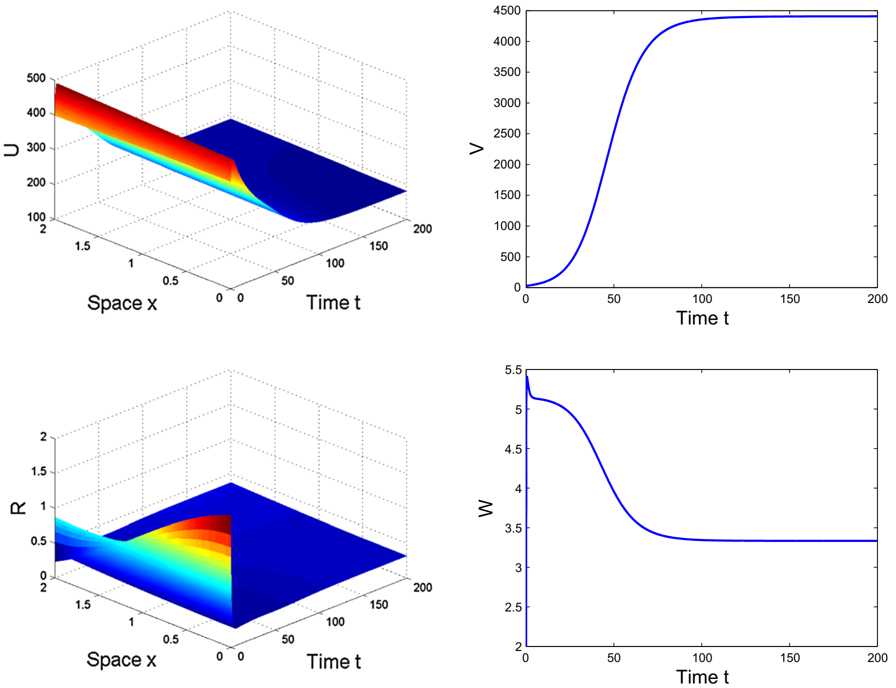


Fig. 6 Coexistence steady state E_4. Here $m_u = 0.1$, $m_v = 0.4$ and other parameters are from Table 1

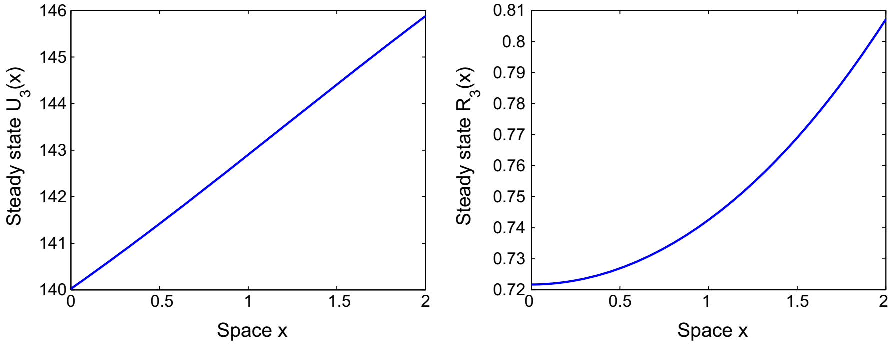


Fig. 7 Profile of pelagic algae-nutrient steady state E_3. Here $m_u = 0.2$, $m_v = 1$ and other parameters are from Table 1. *Left* $U_3(x)$, *Right* $R_3(x)$

pelagic algae, and vice versa (see Fig. 11). This confirms that pelagic algae and benthic algae are able to control each other through the consumption of common resources even if they are located in different spatial positions. Therefore, in the presence of both algae in an aquatic ecosystem, it is possible to prevent the occurance of algal blooms.

The pelagic habitat depth L_1 has no significant effect on pelagic algal biomass and benthic algal biomass (see Fig. 12a), which is partly because that here we do not consider the role of light intensity, which has an important effect on pelagic and benthic

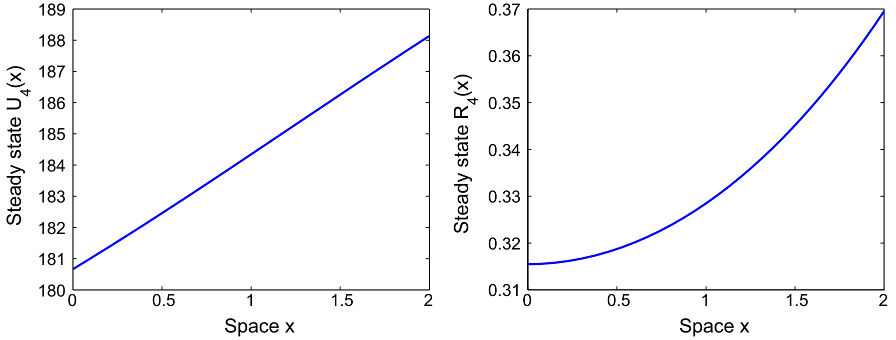


Fig. 8 Profile of coexistence steady state E_4. Here $m_u = 0.1$, $m_v = 0.4$ and other parameters are from Table 1. *Left* $U_4(x)$, *Right* $R_4(x)$

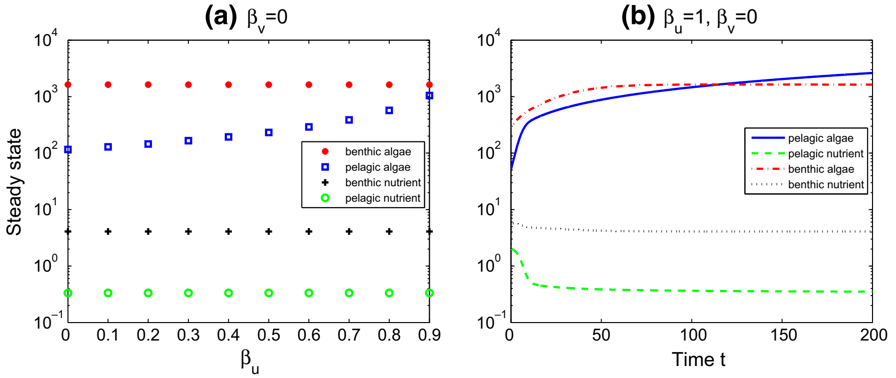


Fig. 9 Influence of nutrient recycling proportion rate β_u on algal biomass density. Here $m_u = 0.1$, $m_v = 0.45$ and other parameters are from Table 1. *Left* Steady state $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $0 \le \beta_u \le 0.9$; *Right* time series of solution for $\beta_u = 1$

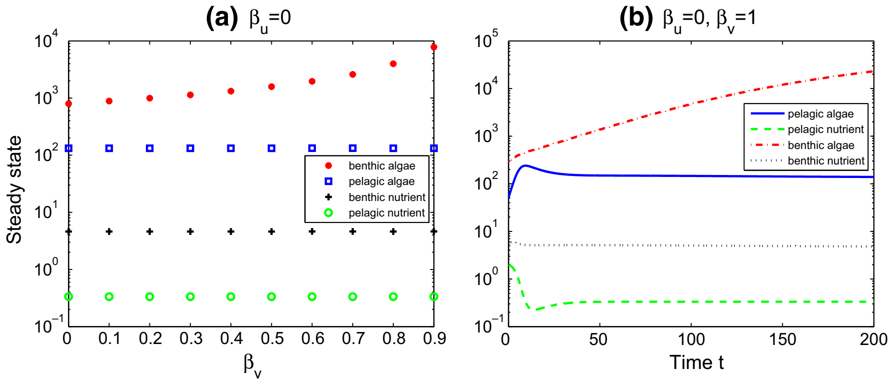


Fig. 10 Influence of nutrient recycling proportion rate β_v on algal biomass density. Here $m_u = 0.1$, $m_v = 0.48$ and other parameters are from Table 1. *Left* Steady state $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $0 \le \beta_v \le 0.9$; *Right* time series of solution for $\beta_v = 1$

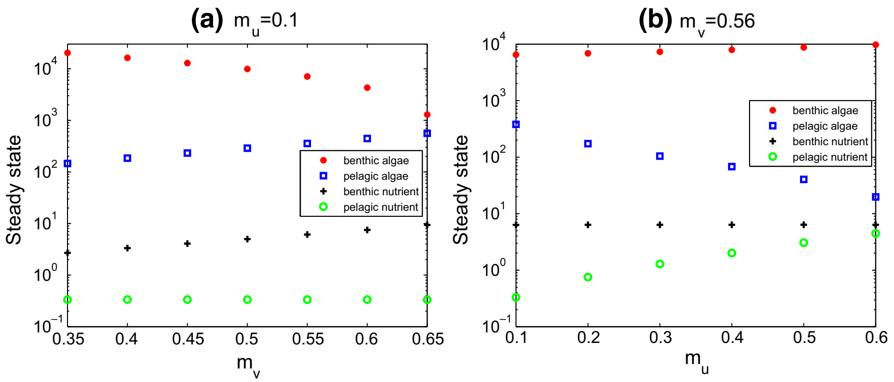


Fig. 11 Influence of parameters m_u, m_v on algal biomass density. Here $W_{sed} = 20$ and other parameters are from Table 1. *Left* Steady state $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $0.35 \le m_v \le 0.65$; *Right* $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $0.1 \le m_u \le 0.6$

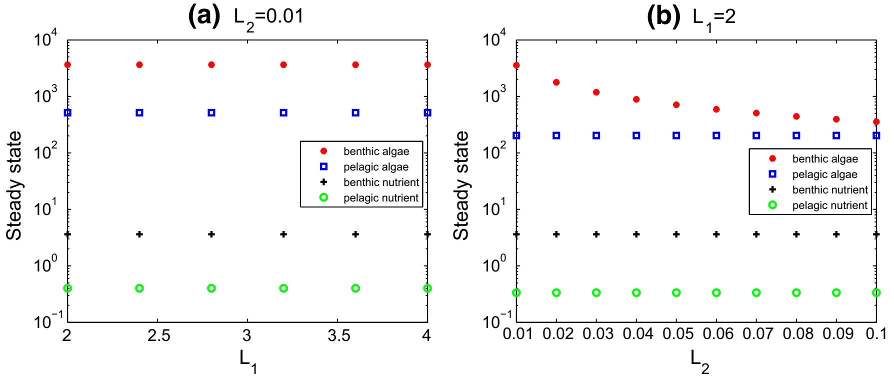


Fig. 12 Influence of parameters L_1, L_2 on algal biomass density. Here $m_v = 0.42$ and other parameters are from Table 1. *Left* Steady state $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $2 \le L_1 \le 4$; *Right* $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $0.01 \le L_2 \le 0.1$

algal biomass. On the other hand, the benthic habitat thickness L_2 has a negative effect on benthic algal biomass density and has no significant effect on pelagic algal biomass since the concentration of dissolved nutrients in the habitat keeps unchange [see (3.34) and Fig. 12b].

Figure 13a shows that an increasing sediment nutrient level (W_{sed}) does not affect pelagic algal biomass, as the concentration of dissolved nutrients in the benthic habitat is always a constant if benthic algae exist [see (3.34) and (3.35)]. Benthic algae increases with respect to W_{sed} as shown in (3.34). This further proves that the presence of benthic algae could control pelagic algal biomass.

Finally we consider the effect of spatial parameters s, D_u, D_r on the coexistence steady state algal biomass density. From Figs. 13b and 14, we can observe: (i) when the algae has a tendency of sinking ($s = 5$), then the steady state distribution of pelagic algae is increasing from the water level to the interface of the pelagic and benthic habitat

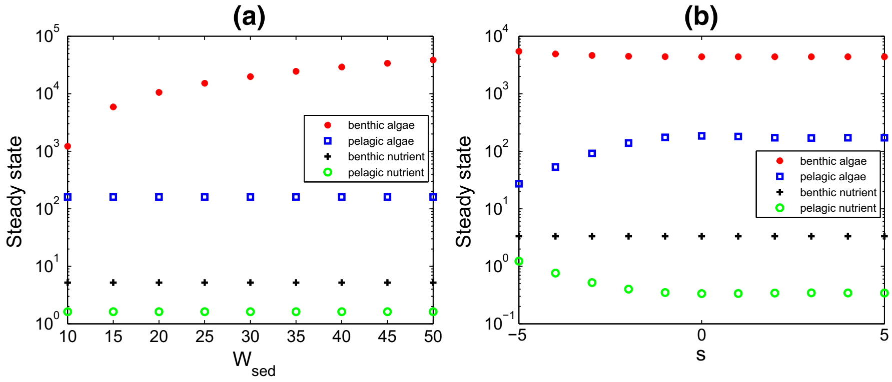


Fig. 13 Influence of parameters W_{sed}, s on algal biomass density. Here **a** $m_u = 0.35, m_v = 0.51$; **b** $m_u = 0.1, m_v = 0.4$. Other parameters are from Table 1. *Left* Steady state $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $10 \leq W_{sed} \leq 50$; *Right* $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $-5 \leq s \leq 5$

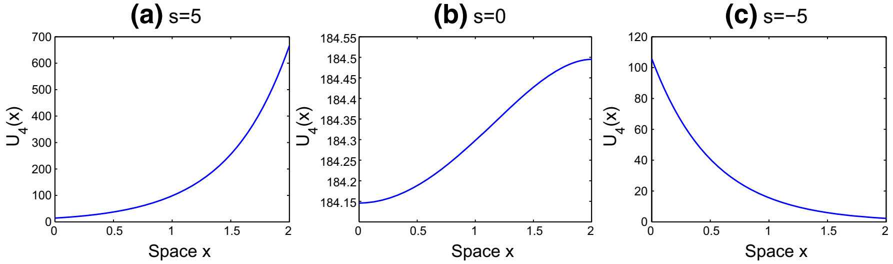


Fig. 14 Profile of steady state $U_4(x)$. Here $m_v = 0.4$ and other parameters are from Table 1

(see Fig. 14a); (ii) when there is no any active movement for pelagic algae ($s = 0$), then the pelagic algal biomass almost distribute evenly in the habitat (see Fig. 14b); and (iii) when pelagic algae has a clear upward trend, the pelagic algal biomass has a decreasing profile and concentrates near the water surface (see Fig. 14c). Similar to the earlier observation and studies in Klausmeier and Litchman (2001) and Du and Hsu (2008b), our studies also suggest that there could be a significant concentration of pelagic algae when the active movement is more pronounced. Moreover, in an oligotrophic shallow aquatic ecosystem with ample supply of light, this upward movement trend can cause a negative effect for pelagic algal biomass (see Fig. 13b).

For the effect of the diffusion coefficients D_u and D_r on algal biomass density, we first consider the case of low nutrient diffusion ($D_r = 0.001$). From Fig. 15a, one can observe that pelagic algal biomass density decreases gradually with the increase of pelagic algal diffusion. When the diffusion coefficient D_u is large, the pelagic algal biomass tends to an asymptote. On the other hand if the nutrient diffusion coefficient is relatively large ($D_r = 2.59$), then Fig. 15b shows that the total pelagic algal biomass does not change significantly with the increase of the turbulent diffusion coefficient D_u.

As a summary of the above discussion, the influence of environmental parameters on algal biomass density are listed in Table 3.

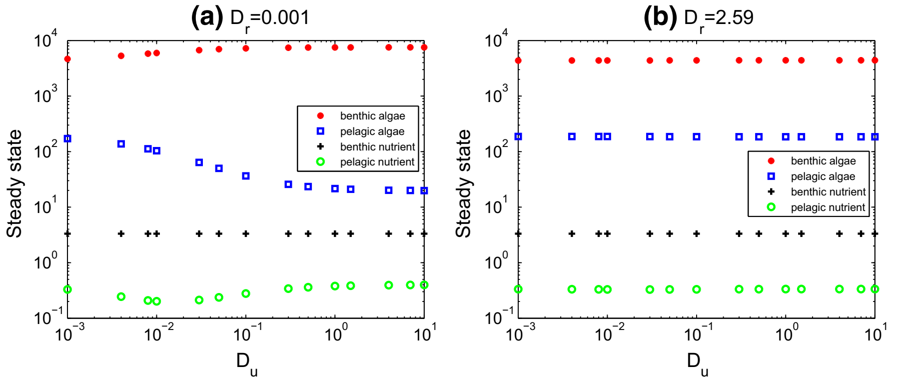


Fig. 15 Influence of parameters D_u, D_r on algal biomass density. Here $m_v = 0.4$ and other parameters are from Table 1. Steady state $(\overline{U}_4, V_4, \overline{R}_4, W_4)$ for $0.001 \le D_u \le 10$

Table 3 The influence of environmental parameters on algal biomass density

Parameters	PABMD	BABD	Parameters	PABMD	BABD
$\beta_u \uparrow$	↑	NSE	$\beta_v \uparrow$	NSE	↑
$m_u \uparrow$	↓	↑	$m_v \uparrow$	↑	↓
$L_1 \uparrow$	NSE	NSE	$L_2 \uparrow$	NSE	↓
$W_{sed} \uparrow$	NSE	↑	$s \uparrow$	↑	NSE
$D_u \uparrow$ D_r is small	↓	↑	$D_u \uparrow$ D_r is large	NSE	NSE

PABMD pelagic algal biomass mean density, *BABD* benthic algal biomass density
↑: increasing, ↓: decreasing, *NSE* no significant effect

5 Discussion

In this paper, we establish and analyze a coupled system of ordinary differential equations and partial differential equations (2.5) modelling the interactions of pelagic algae, benthic algae and one essential nutrient in an oligotrophic shallow aquatic ecosystem with ample supply of light.

The steady state solutions of system (2.5) are completely classified rigorously using the parameters (m_u, m_v) (the loss rates of the pelagic and benthic algae), and the results are summarized in Table 2 and Fig. 2. Our theoretical analysis suggests that both pelagic algae and benthic algae are extinct when m_u and m_v are both over some threshold values (see Theorem 3.2). The benthic and pelagic algae are indirectly competing for a shared resource, hence a competition exclusion occurs when m_u is large but m_v is not (benthic algae dominates, see Theorem 3.4), or when m_v is large but m_u is not (pelagic algae dominates, see Theorem 3.8). On the other hand, the pelagic and benthic algae can coexist when both m_u and m_v are below some threshold values (Theorem 3.11), and the parameter range for algae coexistence is robust. Note that we have shown that the existence/nonexistence of any steady state is independent of spatial environmental parameters such as sinking/buoyant rate s and diffusion coefficients D_u, D_r for pelagic algae and nutrients, but these parameters can affect the profile and amplitude of the steady states.

All the environmental parameters could influence the algal biomass density (see Table 3). Our studies show that in the case of high temperature, nutrient recycling from loss of algal biomass can lead to algal biomass density increases dramatically, which is an important factor in the existence and uniqueness of non-negative steady state solutions (Theorems 3.4, 3.8 and 3.11) and the algal blooms process (Figs. 9 and 10). The presence of benthic algae could control the growth of pelagic algal biomass even if the sediment nutrient level is high (Figs. 11, 13a). In an oligotrophic shallow aquatic ecosystem, the upward movement trend of pelagic algae can lead to a negative effect on the pelagic algal biomass (Fig. 13b). In the case of low nutrient diffusion, pelagic algal biomass is a decreasing function of D_u and tends to an asymptote as the diffusion coefficient D_u approaches infinity, but if the nutrient diffusion coefficient is relatively large, then the total pelagic algal biomass does not change much with the increase of D_u (Fig. 15).

Our study here is one of the first quantitative attempts to model the effect of benthic algae and nutrient inputs, which complements and further develops earlier studies of algae population growth in water column. It is important to understand the stability and asymptotic profile of the non-constant steady states E_3 and E_4, which is not considered in this paper. In the context of competition between pelagic algae and benthic algae, it will be of interest to further model some even more intriguing biological questions. For example, pelagic algae and benthic algae compete for light and nutrients simultaneously Huisman et al. (1999, 2006), algaes may compete for two complementary nutrients Hsu et al. (2011), Klausmeier et al. (2007), algae exchange in the pelagic and benthic habitat Jäger and Diehl (2014), Loreau et al. (2003), the effect of toxic plankton species Hsu et al. (2013), Ikeda et al. (2017), Wang et al. (2015), and the effect of zooplankton and fishes Loladze et al. (2000); Lv et al. (2016). Also an important assumption of our study is the light supply is ample and uniform for the system, which is the case for shallow aquatic ecosystem. The combined effect of light and nutrient will be a subject of future study.

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