Mathematical Biology



Phytoplankton-chytrid-zooplankton dynamics via a reaction-diffusion-advection mycoloop model

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Abstract

Mycoloop is an important aquatic food web composed of phytoplankton, chytrids (one dominant group of parasites in aquatic ecosystems), and zooplankton. Chytrids infect phytoplankton and fragment them for easy consumption by zooplankton. The free-living chytrid zoospores are also a food resource for zooplankton. A dynamic reaction-diffusion-advection mycoloop model is proposed to describe the Phytoplankton-chytrid-zooplankton interactions in a poorly mixed aquatic environment. We analyze the dynamics of the mycoloop model to obtain dissipativity, steady state solutions, and persistence. We rigorously derive several critical thresholds for phytoplankton or zooplankton invasion and chytrid transmission among phytoplankton. Numerical diagrams show that varying ecological factors affect the formation and breakup of the mycoloop, and zooplankton can inhibit chytrid transmission among phytoplankton. Furthermore, this study suggests that mycoloop may either control or cause phytoplankton blooms.

Keywords Mycoloop · Reaction-diffusion-advection model ·

Phytoplankton-chytrid-zooplankton interactions · Chytrid transmission · Ecological factors · Phytoplankton blooms

Mathematics Subject Classification 92D25 · 92B05 · 35K57

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1 Introduction

Phytoplankton and zooplankton are two important aquatic organisms and essential components of aquatic food webs. Phytoplankton are the most important primary producers in aquatic ecosystems and the foundation of the whole trophic level (Chen et al. 2015; Huisman et al. 2006; Klausmeier and Litchman 2001; Wang et al. 2007; Zhang et al. 2021a). Zooplankton generally refer to the group of animals that live planktonically in the water. They have an important effect on population structure of biological communities. Zooplankton have weak swimming ability and cannot move long distances (Huber et al. 2011; Noss and Lorke 2012). Phytoplankton are one of the important food sources of zooplankton, and together with zooplankton influence the structure and biodiversity of aquatic communities (Loladze et al. 2000; Lv et al. 2016; Ruan 1993; Tao et al. 2021; Zhao et al. 2022).

Chytrid fungal parasites, abbreviated as chytrids, are an important group of aquatic parasites, and widely distributed in various aquatic environments (Frenken et al. 2020a, b). There are over 700 species of chytrids that can infect aquatic organisms (Kagami et al. 2014). This covers most zooplankton and phytoplankton. Chytrids move randomly with turbulence as free-living zoospores in the water. These free-living chytrid zoospores actively search for and infect host cells (Chen et al. 2024; Gerla et al. 2013; Kagami et al. 2014; Miki et al. 2011). Once the infection is successful, chytrids absorb nutrients from host cells to develop sporangia. Zoospores are produced in the sporangia and are released into the water to infect new hosts when the sporangia mature (Chen et al. 2024; Gerla et al. 2013; Kagami et al. 2014; Miki et al. 2011).

In this study, we only consider chytrids that infect phytoplankton. Phytoplankton infected by chytrid zoospores exhibit two characteristics. One is that infected phytoplankton cannot reproduce since chytrids consume all organic matter in phytoplankton cells for the development of sporangia (Frenken et al. 2020a; Gerla et al. 2013). When the sporangia mature, they release new free-living zoospores and cause the death of phytoplankton. The other is that chytrid infections can lead to fragmentation of inedible phytoplankton, which become more edible to zooplankton (Frenken et al. 2020a, b; Kagami et al. 2014). A noteworthy phenomenon is that free-living chytrid zoospores in the water have high nutritional quality and zooplankton can also survive by consuming chytrid zoospores (Frenken et al. 2020a, b; Kagami et al. 2014). This forms a chytrid-induced aquatic food web structure containing multiple predatory processes and one chytrid transmission (see Fig. 1). This chytrid-induced trophic link is known as "mycoloop". The mycoloop has been shown to be widespread in aquatic ecosystems (Frenken et al. 2020a; Kagami et al. 2014). To our knowledge, few mathematical models are formulated to explore the mycoloop between phytoplankton, chytrids and zooplankton. Therefore, one of our research objectives is to derive a dynamic model to describe the mycoloop.

The spatial distribution of plankton is uneven, and this heterogeneity favors plankton ecology and evolution. It is well-recognized that phytoplankton and zooplankton can exhibit strong spatial heterogeneity in the vertical direction when the water column is deep. The reason for phytoplankton heterogeneity is that the uneven spatial distribution of resources, the variation of turbulent intensity in the water, and their own directional



Fig. 1 Diagram of the mycoloop: the interactions between phytoplankton, chytrids and zooplankton

transportation (Grover 2017; Huisman et al. 2006; Klausmeier and Litchman 2001; Zhang et al. 2021a, b). The vertical movement of zooplankton is driven by many factors such as avoiding predation (Gliwicz 1986), turbulence in the water and self-swimming (Huber et al. 2011; Noss and Lorke 2012). These result in an extremely uneven vertical spatial distribution of zooplankton. This suggests that it is essential to contain spatial heterogeneity in the phytoplankton-chytrid-zooplankton interactions.

Motivated by the above considerations, we propose and analyze a dynamic mycoloop model. It characterizes the interactions between phytoplankton, chytrids and zooplankton. The model is comprised of two reaction-diffusion-advection equations and two reaction-diffusion equations. Its contribution is to characterize the mycoloop model with spatial heterogeneity. The structure of the model is relatively complex including multiple predation terms and one chytrid transmission process. This greatly increases the difficulty of mathematical analysis. By exploring dynamical properties of the model, several critical thresholds are rigorously derived. For example, the basic ecological reproductive indices for phytoplankton or zooplankton invasion, the basic reproduction numbers for chytrid transmission.

The mycoloop closely connects phytoplankton, chytrids and zooplankton. The complex structure of the mycoloop plays an important role in aquatic ecosystems (Frenken et al. 2020a, b; Kagami et al. 2014). It is noted that existing studies have shown that ecological factors can influence plankton biomass and community structure (Chen et al. 2015; Ryabov et al. 2010; Yoshiyama et al. 2009; Zhang et al. 2023). This means that it is essential to explore the implications of ecological factors on the mycoloop based on the dynamic model proposed above. We will show the evolution trend in the biomass of phytoplankton, chytrids and zooplankton for varying ecological factors, and elucidate some mechanisms of the mycoloop formation and destruction. In this process, we will reveal the roles of the mycoloop in chytrid transmission and phytoplankton blooms. This paper is organized as follows. We propose a dynamic reaction-diffusionadvection model to describe the mycoloop in Sect. 2. The dynamic analysis of the model is given in Sect. 3. We rigorously derive several critical thresholds for phytoplankton or zooplankton invasion as well as chytrid transmission. In Sect. 4, we investigate the effects of ecological factors on the mycoloop and explore chytrid transmission and phytoplankton blooms in the mycoloop. In the last section, we summarize the main findings and present future research questions.

2 Model

A deep aquatic environment is poorly mixed along the water column. The movements of phytoplankton and free-living chytrid zoospores are affected by the turbulence in the vertical direction (Huisman et al. 2006; Klausmeier and Litchman 2001; Zhang et al. 2021a). Zooplankton mainly exhibit vertical migration (Gliwicz 1986; Huber et al. 2011; Noss and Lorke 2012). Therefore, we only consider the vertical diffusion with water depth. Let the time scale be *t* and the water depth coordinate be *x* with the water column bottom $x = x_h$ and the water surface x = 0. The variables and parameters used in the modeling process can be found in Table 1.

This model is constituted by two reaction-diffusion-advection equations and two reaction-diffusion equations. Phytoplankton are classified as susceptible phytoplankton and infected phytoplankton. S(x, t) and I(x, t) denote the biomass density of susceptible and infected phytoplankton respectively. C(x, t) describes the density of free-living chytrid zoospores in the water. The zoospores move randomly with turbulence and infect phytoplankton cells. The biomass density of zooplankton is denoted as Z(x, t). Zooplankton survive and reproduce by consuming phytoplankton and chytrid zoospores. This trophic level in aquatic food webs induced by chytrids constitutes a mycoloop (Frenken et al. 2020a, b; Kagami et al. 2014).

The dynamics of susceptible and infected phytoplankton are expressed as two reaction-diffusion-advection equations:

$$S_{t} = \text{diffusion} - \text{sinking (buoyant)} + \text{growth} - \text{natural death} - \text{intraspecific competition} - \text{infection} - \text{predation} = d_{p}S_{xx} - vS_{x} + r_{p}S - m_{p}S - \eta S(S + I) - \theta SC - \alpha SZ,$$
$$d_{p}S_{x}(0, t) - vS(0, t) = d_{p}S_{x}(x_{h}, t) - vS(x_{h}, t) = 0,$$
(2.1)

and

$$I_{t} = \text{diffusion} - \text{sinking (buoyant)} + \text{infection}$$

$$- \text{natural death} - \text{bursting death} - \text{predation}$$

$$= d_{p}I_{xx} - vI_{x} + \theta SC - m_{p}I - \omega I - \beta IZ,$$

$$d_{p}I_{x}(0, t) - vI(0, t) = d_{p}I_{x}(x_{h}, t) - vI(x_{h}, t) = 0.$$
(2.2)

Here there are two types of movement in phytoplankton: one type is diffusion in the vertical direction induced by the turbulence (Huisman et al. 2006; Klausmeier and

Image Time variables day X Depth m cells/L I Density of infected phytoplankton variables cells/L C Density of infected phytoplankton variables cells/L Z Density of infected phytoplankton variables cells/L Z Density of free-living chyrrid zoospores variables cells/L Z Density of free-living chyrrid zoospores 0.3 (0.05-5) m ² /day Grover (2017); Huisman et al. (2001); Kalasmeter and L dp Vertical turbulent diffusivity of chyrrid 0.3 (0.05-5) m ² /day Grover (2017); Huisman et al. (2001); Kalasmeter and L de Vertical turbulent diffusivity of chyrrid 0.3 (0.05-5) m ² /day Grover (2017); Huisman et al. (2001); Kalasmeter and L de Vertical turbulent diffusivity of cooplankton 0.3 (0.05-5) m ² /day Grover (2017); Huisman et al. (2001); Kalasmeter and L de Vertical turbulent diffusivity of cooplankton 0.3 (0.05-5) m ² /day Grover (2017); Huisman et al. (2001); Kalasmeter and L de Vertical turbulent diffusivity of cooplankton 0.3 (0.05-5) <th>Symbol</th> <th>Meaning</th> <th>Values</th> <th>Units</th> <th>Source</th>	Symbol	Meaning	Values	Units	Source
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	m_p	Death rate of phytoplankton	0.1	day ⁻¹	Jäger et al. (2010); Wang et al. (2007)
θ Infection rate between susceptible 5×10^{-4} (cells/L) ⁻¹ day ⁻¹ Assumption phytoplankton and chytrid zoospores	μ	Intraspecific competition coefficient	10^{-4}	(cells/L) ⁻¹ day ⁻¹	Assumption
	θ	Infection rate between susceptible phytoplankton and chytrid zoospores	5×10^{-4}	(cells/L) ⁻¹ day ⁻¹	Assumption

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Table 1 continue	p			
Symbol	Meaning	Values	Units	Source
З	Bursting death rate of infected phytoplankton due to sporangia maturation	0.6	day ⁻¹	Gerla et al. (2013)
d	Number of newly produced zoospores per phytoplankton cell	8	cells/cell	Gerla et al. (2013)
m_c	Death rate of chytrid zoospores	0.4	day-1	Gerla et al. (2013)
α	Predation rate of zooplankton for susceptible phytoplankton	10^{-4}	(cells/L) ⁻¹ day ⁻¹	Assumption
β	Predation rate of zooplankton for infected phytoplankton	3×10^{-4}	(cells/L) ⁻¹ day ⁻¹	Assumption
×	Predation rate of zooplankton for chytrid zoospores	2×10^{-4}	(cells/L) ⁻¹ day ⁻¹	Assumption
e_p	Efficiency of captured phytoplankton conversion to growth of zooplankton	0.4		Lv et al. (2016)
e_{C}	Efficiency of captured chytrid zoospores conversion to growth of zooplankton	0.5		Miki et al. (2011)
² <i>m</i>	Loss rate of zooplankton	0.2(0.05 - 0.5)	day ⁻¹	Loladze et al. (2000); Miki et al. (2011); Tao et al. (2021)
u_X	Depth of the water column	10	m	Yan et al. (2022)

Litchman 2001; Zhang et al. 2021a), and the other type is sinking (v > 0) or buoyant (v < 0) caused by gravity or the search for the optimal growth position (Grover 2017; Jäger et al. 2010; Ryabov et al. 2010). Based on the research work in Frenken et al. (2020a); Gerla et al. (2013), we assume that both susceptible and infected phytoplankton consume resources, resulting in intraspecific competition with $\eta S(S+I)$. However, only susceptible phytoplankton can reproduce with $r_p S$, while the organic matter produced by infected phytoplankton is consumed by chytrids to develop sporangia. The infection between susceptible phytoplankton and free-living chytrid zoospores is based on the law of mass action with θSC . The reductions of phytoplankton biomass include natural death $(m_p S \text{ and } m_p I)$, bursting mortality induced by sporangia maturation (ωI), and zooplankton predation (αSZ and βIZ). Phytoplankton fragmentation becomes more edible to zooplankton as a result of chytrid infection, leading to the assumption that $\alpha \leq \beta$ (Frenken et al. 2020b). We also assume that no phytoplankton crosses the upper and lower boundaries of the water column. This means that it is no-flux boundary conditions for phytoplankton (Huisman et al. 2006; Klausmeier and Litchman 2001; Zhang et al. 2021a).

The dynamics of free-living chytrid zoospores and zooplankton are described as two reaction-diffusion equations:

$$C_{t} = \text{diffusion} + \text{release of mature sporangia} - \text{death} - \text{infection} - \text{predation}$$

$$= d_{c}C_{xx} + q\omega I - m_{c}C - \theta SC - \gamma CZ, \qquad (2.3)$$

$$C_{x}(0, t) = C_{x}(x_{h}, t) = 0,$$

and

$$Z_{t} = \text{diffusion} + \text{reproduction} - \text{loss}$$

= $d_{z}Z_{xx} + (e_{p}(\alpha S + \beta I) + e_{c}\gamma C) Z - m_{z}Z,$ (2.4)
 $Z_{x}(0, t) = Z_{x}(x_{h}, t) = 0.$

Here the transport of free-living chytrid zoospores is driven by the turbulence with a diffusion rate d_c . Chytrid zoospores in the water column originate from the release of mature chytrid sporangia within infected phytoplankton cells with $q\omega I$ (Frenken et al. 2020a, b). The loss of chytrid zoospores contains three components: death $(m_c C)$, infection (θSC) and predation by zooplankton (γCZ) . Zooplankton move vertically in the water column with a diffusion rate d_z (Tao et al. 2021). Zooplankton reproduction is owing to predation on phytoplankton and free-living chytrid zoospores with $(e_p(\alpha S + \beta I) + e_c\gamma C)Z$. The loss in zooplankton biomass is attributed to mortality and predation. Neumann boundary conditions imply that the water column is closed to chytrid zoospores and zooplankton.

Coupling the equations (2.1)-(2.4), we derive the mycoloop model for phytoplanktonchytrid-zooplankton interactions:

$$\begin{split} S_t &= d_p S_{xx} - v S_x + r_p S - m_p S - \eta S(S+I) - \theta SC - \alpha SZ, \ x \in (0, x_h), \ t > 0, \\ I_t &= d_p I_{xx} - v I_x + \theta SC - m_p I - \omega I - \beta IZ, \ x \in (0, x_h), \ t > 0, \\ C_t &= d_c C_{xx} + q \omega I - m_c C - \theta SC - \gamma CZ, \ x \in (0, x_h), \ t > 0, \end{split}$$

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$$Z_t = d_z Z_{xx} + (e_p(\alpha S + \beta I) + e_c \gamma C) Z - m_z Z, \ x \in (0, x_h), \ t > 0$$
(2.5)

with the boundary conditions

$$d_p S_x(0, t) - vS(0, t) = d_p S_x(x_h, t) - vS(x_h, t) = 0, \ t > 0,$$

$$d_p I_x(0, t) - vI(0, t) = d_p I_x(x_h, t) - vI(x_h, t) = 0, \ t > 0,$$

$$C_x(0, t) = C_x(x_h, t) = 0, \ Z_x(0, t) = Z_x(x_h, t) = 0 \ t > 0$$
(2.6)

and the initial values

$$S(x, 0) = S_0(x) \ge \neq 0, \ I(x, 0) = I_0(x) \ge \neq 0, C(x, 0) = C_0(x) \ge \neq 0, \ Z(x, 0) = Z_0(x) \ge \neq 0, \ x \in [0, x_h].$$
(2.7)

The model parameters are all positive constants except $v \in \mathbb{R}$. Model (2.5) is a complicated model with the mycoloop structure. Its dynamic analysis is more difficult due to the inclusion of multiple predation terms and one chytrid transmission. To clarify the mycoloop in aquatic food webs, we will investigate dynamic properties of model (2.5). Several critical thresholds for phytoplankton or zooplankton invasion and chytrid transmission will be obtained by analyzing the dissipativity and steady state solutions.

3 Dynamical analysis

We investigate the dynamics of model (2.5) in this section. The global existence, uniqueness and dissipative properties of solutions are given in Subsect. 3.1. Nonnegative steady state solutions are explored in Subsect. 3.2. Numerical simulation graphics are provided to complement the above theoretical results. The parameter values in the following figures are derived from Table 1 except for some special comments.

3.1 Global existence, uniqueness and dissipativity

We explore the global existence, uniqueness and dissipativity of solutions in model (2.5).

Theorem 3.1 *Model*(2.5)-(2.7) *has a unique global solution* (S(x, t), I(x, t), C(x, t), Z(x, t)) satisfying S(x, t) > 0, I(x, t) > 0, C(x, t) > 0, Z(x, t) > 0 on $[0, x_h] \times (0, \infty)$, and it is dissipative.

Proof Following the standard arguments in Martin and Smith (1990), it is easy to show that model (2.5)-(2.7) admits a unique local nonnegative solution (S, I, C, Z). From the maximum principle, S(x, t) > 0, I(x, t) > 0, C(x, t) > 0, Z(x, t) > 0. To obtain the global existence of the solutions, we only need to show that the solutions are dissipative.

Let $\tilde{S} = Se^{-(v/d_p)x}$. By the *S* equation in (2.5), we obtain

$$\tilde{S}_{t} \leq d_{p}\tilde{S}_{xx} + v\tilde{S}_{x} + r_{p}\tilde{S} - \eta\tilde{S}^{2}e^{(v/d_{p})x}, \ x \in (0, x_{h}), \ t > 0,
\tilde{S}_{x}(0, t) = \tilde{S}_{x}(x_{h}, t) = 0, \ t > 0.$$
(3.1)

Then

$$\limsup_{t \to \infty} S(x, t) = \limsup_{t \to \infty} \tilde{S}(x, t) e^{(v/d_p)x} \le \frac{r_p e^{(|v|/d_p)x_h}}{\eta} \text{ on } [0, x_h].$$
(3.2)

For any $\varepsilon > 0$, there is a $T_1 > 0$ satisfying $S(x, t) \le r_p e^{(|v|/d_p)x_h}/\eta + \varepsilon$ on $[0, x_h]$ for all $t \ge T_1$. Let $\tilde{I} = I e^{-(v/d_p)x}$. By adding the *S* equation and the *I* equation, we get

$$\begin{split} (\tilde{S}+\tilde{I})_t \leq & d_p(\tilde{S}+\tilde{I})_{xx} + v(\tilde{S}+\tilde{I})_x + r_p\left(\frac{r_p e^{(|v|/d_p)x_h}}{\eta} + \varepsilon\right) e^{-(v/d_p)x} \\ & -m_p(\tilde{S}+\tilde{I}), \ x \in (0, x_h), \\ (\tilde{S}+\tilde{I})_x(0,t) = (\tilde{S}+\tilde{I})_x(x_h,t) = 0 \end{split}$$

for $t > T_1$. Applying the parabolic comparison theorem gives

$$\limsup_{t \to \infty} I(x, t) \leq \limsup_{t \to \infty} (S + I)(x, t) = \limsup_{t \to \infty} (\tilde{S} + \tilde{I}) e^{(v/d_p)x}$$
$$\leq \frac{r_p^2 e^{2(|v|/d_p)x_h}}{\eta m_p} \text{ on } [0, x_h].$$
(3.3)

For the above $\varepsilon > 0$, we can find $T_2 \ge T_1$ satisfying

$$I(x,t) \leq \frac{r_p^2 e^{2(|v|/d_p)x_h}}{\eta m_p} + \varepsilon, \ x \in [0, x_h], \ t \geq T_2.$$

From the C equation in (2.5), we have

$$C_t \le d_c C_{xx} + q\omega \left(\frac{r_p^2 e^{2(|v|/d_p)x_h}}{\eta m_p} + \varepsilon \right) - m_c C, \ x \in (0, x_h), \ t > T_2,$$

$$C_x(0, t) = C_x(x_h, t) = 0, \ t > T_2.$$

Thus,

$$\limsup_{t \to \infty} C(x, t) \le \frac{q \omega r_p^2 e^{2(|v|/d_p)x_h}}{\eta m_p m_c} \text{ on } [0, x_h].$$
(3.4)

Deringer

J. Zhang et al.

positive constants
$$\mu_i$$
, $i = 1, 2, 3$ depending on the initial value (2.7) such that

$$0 < S(x,t) \le \mu_1, \ 0 < I(x,t) \le \mu_2, \ 0 < C(x,t) \le \mu_3, \ x \in [0,x_h], \ t \ge 0.$$

Let $N(t) = \int_0^{x_h} (e_p(S+I) + e_cC + Z) dx$. A direct calculation yields

$$\frac{dN}{dt} \leq \int_0^{x_h} \left(e_p r_p S + e_c q \omega I \right) dx - \min \left\{ m_p, m_c, m_z \right\} N$$
$$\leq \left(e_p r_p \mu_1 + e_c q \omega \mu_2 \right) x_h - \min \left\{ m_p, m_c, m_z \right\} N,$$

and then

$$N(t) \le N(0)e^{-\min\{m_p, m_c, m_z\}t} + \frac{\left(e_p r_p \mu_1 + e_c q \omega \mu_2\right) x_h}{\min\{m_p, m_c, m_z\}} \left(1 - e^{-\min\{m_p, m_c, m_z\}t}\right).$$
(3.5)

Let $U(t) := \max_{x \in [0,x_h], s \in [0,t]} Z(x, s)$. If Z is not ultimately bounded, then $U(t) \to \infty$ as $t \to \infty$ since U(t) is increasing for t. Then there is a strictly monotone increasing sequence $\{t_i\}_{i=1}^{\infty}$ with $t_1 > 1$ satisfying $U(t_i) = \max_{x \in [0,x_h]} Z(x, t_i) \to \infty$ as $i \to \infty$. Let

$$u_i(x,t) = Z(x,t+t_i-1)/U(t_i),$$

$$v_i(x,t) = e_p(\alpha S(x,t+t_i-1) + \beta I(x,t+t_i-1)) + e_c \gamma C(x,t+t_i-1) - m_z.$$

Hence

$$\begin{aligned} (u_i)_t &= d_z(u_i)_{xx} + v_i(x,t)u_i, \ x \in (0, x_h), \ t > 0, \\ (u_i)_x(0,t) &= (u_i)_x(x_h,t) = 0, \ t > 0, \\ 0 &\le u_i(x,0) \le 1, \ x \in [0, x_h]. \end{aligned}$$

For all $x \in [0, x_h]$ and any $t \ge 0$, we obtain

$$|v_i(x,t)| \le e_p(\alpha \mu_1 + \beta \mu_2) + e_c \gamma \mu_3 + m_z.$$
(3.6)

Then

$$0 < u_i(x, t) < e^{(e_p(\alpha\mu_1 + \beta\mu_2) + e_c\gamma\mu_3 + m_z)t}, x \in [0, x_h], t > 0.$$

This means that $\{u_i\}$ is bounded in $C^{1+\hat{\omega},\hat{\omega}}([0, x_h] \times [1/4, 4])$ for any $\hat{\omega} \in (0, 1)$ by using the standard parabolic regularity. Then we can assume $u_i \to u^*$ in $C^{1,0}([0, x_h] \times [1/4, 4])$ as $i \to \infty$. It follows from (3.6) that $v_i \to v^*$ weakly in $L^2([0, x_h] \times [1/4, 4])$ as $i \to \infty$, and then $|v^*| \le e_p(\alpha \mu_1 + \beta \mu_2) + e_c \gamma \mu_3 + m_z$. Hence u^* satisfies

$$(u^*)_t = d_z(u^*)_{xx} + v^*(x,t)u^*, \ x \in (0,x_h), \ t \in [1/4,4]$$

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$$\begin{aligned} (u^*)_x(0,t) &= (u^*)_x(x_h,t) = 0, \ t \in [1/4,4], \\ 0 &\le u^*(x,t) \le e^{(e_p(\alpha\mu_1 + \beta\mu_2) + e_c\gamma\mu_3 + m_z)t}, \ x \in [0,x_h], \ t \in [1/4,4] \end{aligned}$$

From $\max_{x \in [0,x_h]} u_i(x, 1) = 1$, we have $\max_{x \in [0,x_h]} u^*(x, 1) = 1$ and $u^* \ge \neq 0$. Then $u^*(x, 1) \ge \omega_0 > 0$ on $[0, x_h]$ for some positive constant ω_0 by using the strong maximum principle. Hence, $u_i(x, 1) \ge \omega_0/2 > 0$ on $[0, x_h]$ if *i* is sufficiently large. It follows that $Z(x, t_i) = u_i(x, 1)U(t_i) \ge (\omega_0/2)U(t_i)$ on $[0, x_h]$ for sufficiently large *i*. Hence,

$$N(t_i) \ge \int_0^{x_h} Z(x, t_i) dx \ge \frac{\omega_0 x_h}{2} U(t_i) \to \infty \text{ as } i \to \infty.$$

It is a contradiction to (3.5), and then the claim holds. This completes the proof. \Box

Remark 3.2 Let

$$X := \{ (S, I, C, Z) \in C([0, x_h], \mathbb{R}^4) : S(\cdot) \ge 0, I(\cdot) \ge 0, C(\cdot) \ge 0, Z(\cdot) \ge 0 \}$$

In symbol, $X = C([0, x_h], \mathbb{R}^4_+)$. By Theorem 3.1, the system (2.5) generates a semiflow $\Psi(t) : X \to X$ by

$$\Psi(t)(v_0)(x) = (S(x, t, v_0), I(x, t, v_0), C(x, t, v_0), Z(x, t, v_0)), \ x \in [0, x_h], \ t \ge 0,$$
(3.7)

for each $v_0 = (S_0, I_0, C_0, Z_0) \in X$, and it is point dissipative.

3.2 Steady state solutions

Model (2.5) has five types of nonnegative steady state solutions: Extinction steady state $E_0 = (0, 0, 0, 0)$. Phytoplankton-only steady state $E_1 = (S_1(x), 0, 0, 0)$, where $S_1(x)$ satisfies

$$d_p S'' - v S' + (r_p - m_p) S - \eta S^2 = 0, \ x \in (0, x_h),$$

$$d_p S'(0) - v S(0) = d_p S'(x_h) - v S(x_h) = 0.$$

Phytoplankton-zooplankton-only steady state $E_2 = (S_2(x), 0, 0, Z_2(x))$, where $S_2(x), Z_2(x)$ satisfy

$$d_p S'' - vS' + (r_p - m_p)S - \eta S^2 - \alpha SZ = 0, \ x \in (0, x_h),$$

$$d_z Z'' + e_p \alpha SZ - m_z Z = 0, \ x \in (0, x_h),$$

$$d_p S'(0) - vS(0) = d_p S'(x_h) - vS(x_h) = 0,$$

$$Z'(0) = Z'(x_h) = 0.$$

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Endemic steady state without zooplankton $E_3 = (S_3(x), I_3(x), C_3(x), 0)$, where $S_3(x), I_3(x), C_3(x)$ satisfy

$$d_{p}S'' - vS' + (r_{p} - m_{p})S - \eta S(S + I) - \theta SC = 0, \ x \in (0, x_{h}),$$

$$d_{p}I'' - vI' + \theta SC - (m_{p} + \omega)I = 0, \ x \in (0, x_{h}),$$

$$d_{c}C'' + q\omega I - m_{c}C - \theta SC = 0, \ x \in (0, x_{h}),$$

$$d_{p}S'(0) - vS(0) = d_{p}S'(x_{h}) - vS(x_{h}) = 0,$$

$$d_{p}I'(0) - vI(0) = d_{p}I'(x_{h}) - vI(x_{h}) = 0,$$

$$C'(0) = C'(x_{h}) = 0.$$

(3.8)

Endemic steady state with zooplankton $E_4 = (S_4(x), I_4(x), C_4(x), Z_4(x))$, where $S_4(x), I_4(x), C_4(x), Z_4(x)$ satisfy

$$\begin{aligned} d_p S'' - vS' + (r_p - m_p)S - \eta S(S + I) &- \theta SC - \alpha SZ = 0, \ x \in (0, x_h), \\ d_p I'' - vI' + \theta SC - (m_p + \omega)I - \beta IZ = 0, \ x \in (0, x_h), \\ d_c C'' + q\omega I - m_c C - \theta SC - \gamma CZ = 0, \ x \in (0, x_h), \\ d_z Z'' + (e_p(\alpha S + \beta I) + e_c \gamma C)Z - m_z Z = 0, \ x \in (0, x_h), \\ d_p S'(0) - vS(0) &= d_p S'(x_h) - vS(x_h) = 0, \\ d_p I'(0) - vI(0) &= d_p I'(x_h) - vI(x_h) = 0, \\ C'(0) &= C'(x_h) = 0, \ Z'(0) = Z'(x_h) = 0. \end{aligned}$$
(3.9)

To explore the above steady state solutions, we denote $\lambda_1(l(x), d, v)$ as the principal eigenvalue of

$$d\rho''(x) - v\rho'(x) + l(x)\rho = \lambda\rho, \ x \in (0, x_h), \ d\rho'(0) - v\rho(0) = d\rho'(x_h) - v\rho(x_h) = 0$$
(3.10)

for $l \in L^{\infty}([0, x_h])$. From Proposition 3.1 in Wang et al. (2019), $\lambda_1(l(x), d, v)$ uniquely exists and is increasing with respect to l. If v = 0, then $\lambda_1(l(x), d, 0)$ is denoted as $\lambda_1(l(x), d)$.

Theorem 3.3 E_0 always uniquely exists and it is globally asymptotically stable if $R_p = r_p/m_p < 1$.

Proof It is obvious that E_0 uniquely exists. Consider the eigenvalue problem at E_0

$$\lambda \phi = d_p \phi'' - v \phi' + (r_p - m_p) \phi, \ x \in (0, x_h),$$
(3.11a)

$$\lambda \varphi = d_p \varphi'' - v \varphi' - (m_p + \omega) \varphi, \ x \in (0, x_h), \tag{3.11b}$$

$$\lambda \psi = d_c \psi'' + q \omega \varphi - m_c \psi, \ x \in (0, x_h), \tag{3.11c}$$

$$\lambda \xi = d_z \xi'' - m_z \xi, \ x \in (0, x_h), \tag{3.11d}$$

$$d_p \phi'(0) - v \phi(0) = d_p \phi'(x_h) - v \phi(x_h) = 0, \qquad (3.11e)$$

$$d_p \varphi'(0) - v\varphi(0) = d_p \varphi'(x_h) - v\varphi(x_h) = 0,$$
 (3.11f)

$$\psi'(0) = \psi'(x_h) = 0,$$
 (3.11g)

$$\xi'(0) = \xi'(x_h) = 0.$$
 (3.11h)

It is clear that λ is an eigenvalue of (3.11) if and only if λ is an eigenvalue of one of the following four operators

$$d_p \frac{d^2}{dx^2} - v \frac{d}{dx} + r_p - m_p, \ d_p \frac{d^2}{dx^2} - v \frac{d}{dx} - (m_p + \omega), \ d_c \frac{d^2}{dx^2} - m_c, \ d_z \frac{d^2}{dx^2} - m_z$$

with the boundary conditions (3.11e)-(3.11h). All eigenvalues of the operators $d_c \frac{d^2}{dx^2} - m_c$ and $d_z \frac{d^2}{dx^2} - m_z$ with the Neumann boundary condition are less than 0. By (3.10), all eigenvalues of the operator $d_p \frac{d^2}{dx^2} - v \frac{d}{dx} + r_p - m_p$ with (3.11e) are less than 0 if $R_p < 1$ and all eigenvalues of $d_p \frac{d^2}{dx^2} - v \frac{d}{dx} - (m_p + \omega)$ with (3.11f) also are less than 0. The means that E_0 is locally asymptotically stable if $R_p < 1$.

We next need to show E_0 is globally attractive. We let $\tilde{S} = Se^{-(v/d_p)x}$ and have

$$\tilde{S}_{t} \leq d_{p}\tilde{S}_{xx} + v\tilde{S}_{x} + r_{p}\tilde{S} - m_{p}\tilde{S}, \ x \in (0, x_{h}), \ t > 0,
\tilde{S}_{x}(0, t) = \tilde{S}_{x}(x_{h}, t) = 0, \ t > 0.$$

Then

$$\limsup_{t \to \infty} S(x, t) = \limsup_{t \to \infty} \tilde{S}(x, t) e^{(v/d_p)x} = 0 \text{ on } [0, x_h]$$

if $R_p < 1$. Let $\tilde{I} = Ie^{-(v/d_p)x}$. From *S* and *I* equations in model (2.5), for any $\varepsilon > 0$, we have

$$\begin{split} (\tilde{S}+\tilde{I})_t &\leq d_p(\tilde{S}+\tilde{I})_{xx} + v(\tilde{S}+\tilde{I})_x + r_p\varepsilon - m_p(\tilde{S}+\tilde{I}), \ x \in (0, x_h), \\ (\tilde{S}+\tilde{I})_x(0,t) &= (\tilde{S}+\tilde{I})_x(x_h,t)(x_h,t) = 0 \end{split}$$

for sufficiently large t. Thus $\limsup_{t\to\infty} I(x,t) = 0$ on $[0, x_h]$. Similarly, $\limsup_{t\to\infty} C(x,t) = 0$, $\limsup_{t\to\infty} Z(x,t) = 0$ on $[0, x_h]$.

Remark 3.4 Theorem 3.3 explains that the extinction of plankton is inevitable if $R_p < 1$. This indicates that phytoplankton are the foundation of the entire aquatic food webs. Once phytoplankton become extinct, aquatic ecosystems will collapse.

From Proposition 3.2 in Wang et al. (2019), the system

$$S_{t} = d_{p}S_{xx} - vS_{x} + (r_{p} - m_{p})S - \eta S^{2}, \ x \in (0, x_{h}), \ t > 0,$$

$$d_{p}S_{x}(0, t) - vS(0, t) = d_{p}S_{x}(x_{h}, t) - vS(x_{h}, t), \ t > 0$$
(3.12)

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has a unique positive steady state $S_1(x)$ if $R_p > 1$ and it is globally asymptotically stable. This indicates that E_1 uniquely exists if $R_p > 1$. To explore the stability of E_1 , we linearize (2.5) at E_1 and let $\hat{I} = Ie^{-(v/d_p)x}$. Then

$$\begin{split} \hat{I}_t &= d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} S_1 C - (m_p + \omega) \hat{I}, \ x \in (0, x_h), \ t > 0, \\ C_t &= d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - (m_c + \theta S_1) C, \ x \in (0, x_h), \ t > 0, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > 0. \end{split}$$

Consider the linear parabolic system

$$\begin{split} \hat{I}_t &= d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} l_1 C - (m_p + \omega) \hat{I}, \ x \in (0, x_h), \ t > 0, \\ C_t &= d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - (m_c + \theta l_2) C, \ x \in (0, x_h), \ t > 0, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > 0 \end{split}$$

for $l_1, l_2 \in C([0, x_h], \mathbb{R}_+)$. Denote $\Pi^{l_2}(t) : C([0, x_h], \mathbb{R}^2) \to C([0, x_h], \mathbb{R}^2)$ as the solution semigroup generated by

$$\hat{I}_{t} = d_{p}\hat{I}_{xx} + v\hat{I}_{x} - (m_{p} + \omega)\hat{I}, \ x \in (0, x_{h}), \ t > 0, C_{t} = d_{c}C_{xx} + q\omega e^{(v/d_{p})x}\hat{I} - (m_{c} + \theta l_{2})C, \ x \in (0, x_{h}), \ t > 0,$$
 (3.13)
$$\hat{I}_{x}(0, t) = \hat{I}_{x}(x_{h}, t) = C_{x}(0, t) = C_{x}(x_{h}, t) = 0, \ t > 0.$$

It follows that the solution distribution at time *t* is $\Pi^{l_2}(t)(\zeta_1(x), \zeta_2(x))$, where $\hat{I}(x, 0) = \zeta_1(x), C(x, 0) = \zeta_2(x)$. Define

$$\mathcal{F}^{l_1}(x) = \begin{pmatrix} 0 \ \theta e^{-(v/d_p)x} l_1 \\ 0 \ 0 \end{pmatrix}.$$
 (3.14)

One can derive the next generation operator $H^{(l_1,l_2)}$ as

$$H^{(l_1,l_2)}(\zeta_1,\zeta_2)(x) = \int_0^\infty \mathcal{F}^{l_1}(x)\Pi^{l_2}(t)(\zeta_1(x),\zeta_2(x))dt,$$

which describes the distribution of total new infected phytoplankton when zooplankton are absent. Thus, the basic reproduction number associated with (l_1, l_2) is denoted as

$$R_0(l_1, l_2) = r\left(H^{(l_1, l_2)}\right)$$

where $r(H^{(l_1,l_2)})$ is the spectral radius. If $l_1 = l_2 = S_1$, then the basic reproduction number for chytrid transmission without zooplankton is expressed as

$$R_0 := R_0(S_1, S_1).$$

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Consider the eigenvalue problem

$$\lambda \varphi = d_p \varphi'' + v \varphi' + \theta e^{-(v/d_p)x} l_1 \psi - (m_p + \omega) \varphi, \ x \in (0, x_h),$$

$$\lambda \psi = d_c \psi'' + q \omega e^{(v/d_p)x} \varphi - (m_c + \theta l_2) \psi, \ x \in (0, x_h),$$

$$\varphi'(0) = \varphi'(x_h) = \psi'(0) = \psi'(x_h) = 0.$$

(3.15)

It is clear that (3.15) is a cooperation system. Following Krein-Rutman theorem, there exists a unique principal eigenvalue $\lambda_1(l_1, l_2)$ with a strongly positive eigenfunction $(\hat{\varphi}, \hat{\psi})$ satisfying (3.15). According to Theorem 3.1 (i) in Wang and Zhao (2012), the following conclusion holds.

Lemma 3.5 $\lambda_1(l_1, l_2)$ and $R_0(l_1, l_2) - 1$ have the same sign.

Theorem 3.6 E_1 uniquely exists if $R_p > 1$, and it is locally asymptotically stable if

$$R_0 < 1, \ R_z = \frac{\lambda_1(d_z, e_p \alpha S_1)}{m_z} < 1.$$
 (3.16)

Furthermore, together with $R_0(S_1, 0) < 1$, then E_1 is globally asymptotically stable.

Proof Consider the eigenvalue problem at E_1

$$\lambda \phi = d_p \phi'' - v \phi' + (r_p - m_p) \phi - 2\eta S_1 \phi - \eta S_1 \varphi - \theta S_1 \psi - \alpha S_1 \xi, \ x \in (0, x_h),$$
(3.17a)

$$\lambda \varphi = d_p \varphi'' - v \varphi' + \theta S_1 \psi - (m_p + \omega) \varphi, \ x \in (0, x_h),$$
(3.17b)

$$\lambda \psi = d_c \psi''(x) + q \omega \varphi - m_c \psi - \theta S_1 \psi, \ x \in (0, x_h), \tag{3.17c}$$

$$\lambda \xi = d_z \xi'' + (e_p \alpha S_1 - m_z) \xi, \ x \in (0, x_h), \tag{3.17d}$$

$$d_p \phi'(0) - v \phi(0) = d_p \phi'(x_h) - v \phi(x_h) = 0, \qquad (3.17e)$$

$$d_p \varphi'(0) - v\varphi(0) = d_p \varphi'(x_h) - v\varphi(x_h) = 0, \qquad (3.17f)$$

$$\psi'(0) = \psi'(x_h) = 0,$$
 (3.17g)

$$\xi'(0) = \xi'(x_h) = 0. \tag{3.17h}$$

Let λ_{\max} be the eigenvalue of the largest real part of (3.17). If $\varphi \neq 0$ or $\psi \neq 0$ or $\xi \neq 0$, from (3.17b)-(3.17d) and the boundary conditions (3.17f)-(3.17h), we have $\lambda_{\max} = \max\{\lambda_1(S_1, S_1), \lambda_1(d_z, e_p \alpha S_1) - m_z\} < 0$ if (3.16) holds. If $\varphi = 0, \psi = 0$ and $\xi = 0$, by (3.17a) and its boundary condition (3.17e), we obtain

$$\lambda_{\max} = \lambda_1 \left(d_p, v, r_p - m_p - 2\eta S_1 \right) < \lambda_1 \left(d_p, v, r_p - m_p - \eta S_1 \right) = 0.$$

The above analysis implies that E_1 is locally asymptotically stable if (3.16) holds.

To obtain the global stability, it only needs to prove that E_1 is globally attractive. From (3.12), $\limsup_{t\to\infty} S(x,t) \leq S_1(x)$ on $[0, x_h]$ since $R_p > 1$. For any $\varepsilon > 0$, we can find a $t_1 > 0$ satisfying $S(x,t) \leq S_1(x) + \varepsilon$ on $[0, x_h]$ for all $t > t_1$. Let $l_1 = S_1 + \varepsilon$, $l_2 = 0$ in (3.15). It follows that there is a unique principal eigenvalue $\lambda_1(S_1 + \varepsilon, 0) < 0$ if $R_0(S_1, 0) < 1$, and it has a strongly positive eigenfunction $(\hat{\varphi}^{\varepsilon}, \hat{\psi}^{\varepsilon})$. By *I* and *C* equations in (2.5), letting $\hat{I} = Ie^{-(v/d_p)x}$, we have

$$\begin{split} \hat{I}_t &\leq d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} (S_1 + \varepsilon) C - (m_p + \omega) \hat{I}, \ x \in (0, x_h), \ t > t_1, \\ C_t &\leq d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - m_c C, \ x \in (0, x_h), \ t > t_1, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > t_1. \end{split}$$

There exists a sufficiently large positive constant L_0 such that $(\hat{I}(x, t_1), C(x, t_1)) \le L_0(\hat{\varphi}^{\varepsilon}, \hat{\psi}^{\varepsilon})$. It is noted that $L_0 e^{\lambda_1(S_1 + \varepsilon, 0)(t - t_1)}(\hat{\varphi}^{\varepsilon}, \hat{\psi}^{\varepsilon})$ is a solution of

$$\begin{split} \hat{I}_t &= d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} (S_1 + \varepsilon) C - (m_p + \omega) \hat{I}, \ x \in (0, x_h), \ t > t_1, \\ C_t &= d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - m_c C, \ x \in (0, x_h), \ t > t_1, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > t_1. \end{split}$$

From the comparison theorem, we get

$$\left(\hat{I}(x,t),C(x,t)\right) \le L_0 e^{\lambda_1 (S_1 + \varepsilon, 0)(t-t_1)} \left(\hat{\varphi}^{\varepsilon}, \hat{\psi}^{\varepsilon}\right), \ x \in [0, x_h], \ t \ge t_1.$$

This shows that $\limsup_{t\to\infty} I(x,t) = \limsup_{t\to\infty} \hat{I}(x,t)e^{(v/d_p)x} = 0$ and $\limsup_{t\to\infty} C(x,t) = 0$ on $[0, x_h]$ from $\lambda_1(S_1 + \varepsilon, 0) < 0$. For the above $\varepsilon > 0$, we can find a $t_2 \ge t_1$ satisfying $I(x,t) \le \varepsilon$ and $C(x,t) \le \varepsilon$ on $[0, x_h]$ for any $t > t_2$. From $R_z < 1$, $R_z^{\varepsilon} = \lambda_1(d_z, e_p(\alpha(S_1 + \varepsilon) + \beta\varepsilon) + e_c\gamma\varepsilon)/m_z < 1$. By the Z equation in model (2.5), we get

$$Z_t \le d_z Z_{xx} + \left(e_p \left(\alpha(S_1 + \varepsilon) + \beta \varepsilon \right) + e_c \gamma \varepsilon - m_z \right) Z, \ x \in (0, x_h), \ t > t_2,$$

$$Z_x(0, t) = Z_x(x_h, t) = 0, \ t > t_2.$$

Then $\limsup_{t\to\infty} Z(x, t) = 0$ on $[0, x_h]$ from $R_z^{\varepsilon} < 1$. Applying Theorem 1.8 in Mischaikow et al. (1995) or Theorem 4.1 in Thieme (1992), the *S* equation in model (2.5) reduces to (3.12). Then $\limsup_{t\to\infty} S(x, t) = S_1(x)$ on $[0, x_h]$, and then E_1 is globally attractive. The proof is complete.

Remark 3.7 R_p is the basic ecological reproductive index for phytoplankton invasion. It evaluates the viability of phytoplankton. $R_p < 1$ means phytoplankton are extinct, while $R_p > 1$ indicates phytoplankton can survive in aquatic ecosystems. We only give that E_1 is globally asymptotically stable when $R_0(S_1, 0) < 1$, and indeed this conclusion is also true if $R_0 < 1$ from numerical simulations.

To investigate the existence of E_2 , we consider the phytoplankton-zooplankton interaction model

$$S_{t} = d_{p}S_{xx} - vS_{x} + r_{p}S - m_{p}S - \eta S^{2} - \alpha SZ, \ x \in (0, x_{h}), \ t > 0,$$

$$Z_{t} = d_{z}Z_{xx} + e_{p}\alpha SZ - m_{z}Z, \ x \in (0, x_{h}), \ t > 0,$$

$$d_{p}S_{x}(0, t) - vS(0, t) = d_{p}S_{x}(x_{h}, t) - vS(x_{h}, t) = 0, \ t > 0,$$

$$Z_{x}(0, t) = Z_{x}(x_{h}, t) = 0, \ t > 0.$$
(3.18)

Let $(S(x, t, (S_0, Z_0)), Z(x, t, (S_0, Z_0)))$ satisfy (3.18) with $(S_0, Z_0) \in C([0, x_h], \mathbb{R}^2_+)$. Denote the solution semiflow $\Sigma(t) : C([0, x_h], \mathbb{R}^2_+) \to C([0, x_h], \mathbb{R}^2_+)$ by

$$\Sigma(t)(S_0, Z_0)(x) = (S(x, t, (S_0, Z_0)), Z(x, t, (S_0, Z_0))), x \in [0, x_h], t \ge 0.$$

Let

 $H_0 := \{ (S, Z) \in C([0, x_h], \mathbb{R}^2_+) : S(\cdot) \neq 0, \ Z(\cdot) \neq 0 \}, \ \partial H_0 = C([0, x_h], \mathbb{R}^2_+) \setminus H_0.$

The following result is derived from Theorem 3.9 in Wang and Nie (2022) and Theorem 2.1 in Nie et al. (2023).

Lemma 3.8 If $R_p > 1$ and $R_z > 1$, model (3.18) is uniformly persistent for $(H_0, \partial H_0)$. Furthermore, model (3.18) has a global attractor $\Delta_1 \subset \text{Int } H_0$ satisfying $\Sigma(t)(\Delta_1) = \Delta_1$, and a unique positive steady state (S_2, Z_2) .

The conclusion about the existence of E_2 comes directly from Lemma 3.8.

Theorem 3.9 Model (2.5) has a unique phytoplankton-zooplankton-only steady state E_2 if $R_p > 1$ and $R_z > 1$.

- **Remark 3.10** 1. R_z is the basic ecological reproductive index for zooplankton invasion without chytrid infection. Theorem 3.9 indicates that $R_z = 1$ is the critical threshold for zooplankton survival. $R_z > 1$ means successful zooplankton invasion, conversely, $R_z < 1$ means failed invasion. It is difficult to obtain the stability of E_2 because of the complex structure of model (2.5). When the intraspecific competition coefficient η decreases, numerical analysis shows that E_2 loses its stability in the (*S*, *Z*) plane. It results in a spatially inhomogeneous boundary periodic solution (see Fig. 2). This implies that the paradox of nutrient enrichment can happen.
- 2. From Lemma 2.2 in Nie et al. (2020) or Lemma 3.1 in Nie et al. (2023), R_z is strictly decreasing for $d_z > 0$ with $\lim_{d_z \to 0^+} R_z = e_p \alpha \max_{x \in [0, x_h]} S_1(x)/m_z$ (see Fig. 3b). This means that the reduction in the random diffusion of zooplankton favors its invasion. From Fig. 3a and c, one can observe that R_z is non-monotonic with respect to d_p and v, and there may be multiple critical thresholds for zooplankton survival/extinction. The method used here to calculate the principal eigenvalues is taken from the appendix in Zhou and Huang (2022).



Fig. 2 The spatially inhomogeneous boundary periodic solution for the phytoplankton-zooplankton coexistence. Here $\eta = 10^{-8}$, $m_z = 0.1$



Fig. 3 Dependence of R_z on the spatial factors d_p , d_z , v. Here $m_z = 0.36$, $\mathbf{a} d_z = 0.5$ $\mathbf{b} d_p = 0.1$ $\mathbf{c} d_p = 0.1$, $d_z = 0.7$

To obtain the existence of E_3 , we consider the phytoplankton-chytrid interaction model:

$$S_{t} = d_{p}S_{xx} - vS_{x} + r_{p}S - m_{p}S - \eta S(S + I) - \theta SC, \ x \in (0, x_{h}), \ t > 0,$$

$$I_{t} = d_{p}I_{xx} - vI_{x} + \theta SC - (m_{p} + \omega)I, \ x \in (0, x_{h}), \ t > 0,$$

$$C_{t} = d_{c}C_{xx} + q\omega I - m_{c}C - \theta SC, \ x \in (0, x_{h}), \ t > 0,$$

$$d_{p}S_{x}(0, t) - vS(0, t) = d_{p}S_{x}(x_{h}, t) - vS(x_{h}, t) = 0, \ t > 0,$$

$$d_{p}I_{x}(0, t) - vI(0, t) = d_{p}I_{x}(x_{h}, t) - vI(x_{h}, t) = 0, \ t > 0,$$

$$C_{x}(0, t) = C_{x}(x_{h}, t) = 0, \ t > 0.$$
(3.19)

Let $(S(x, t, (S_0, I_0, C_0)), I(x, t, (S_0, I_0, C_0)), C(x, t, (S_0, I_0, C_0)))$ satisfy (3.19) with $(S_0, I_0, C_0) \in C([0, x_h], \mathbb{R}^3_+)$. Denote the solution semiflow $\Lambda(t) : C([0, x_h], \mathbb{R}^3_+) \rightarrow C([0, x_h], \mathbb{R}^3_+)$ by

$$\Lambda(t)(S_0, I_0, C_0)(x) = (S(x, t, (S_0, I_0, C_0)), I(x, t, (S_0, I_0, C_0)), C(x, t, (S_0, I_0, C_0))),$$

for $x \in [0, x_h]$ and $t \ge 0$. Define

$$Y_0 := \{ (S, I, C) \in C([0, x_h], \mathbb{R}^3_+) : S(\cdot) \neq 0, I(\cdot) \neq 0, C(\cdot) \neq 0 \}$$
$$\partial Y_0 = C([0, x_h], \mathbb{R}^3_+) \setminus Y_0.$$

The following Lemma shows that $R_0 = 1$ is a critical threshold for chytrid transmission when there are no zooplankton. The proof is given in Appendix.

Lemma 3.11 If $R_p > 1$ and $R_0 > 1$, model (3.19) is uniformly persistent for $(Y_0, \partial Y_0)$. Furthermore, model (3.19) has a global attractor $\Delta_2 \subset \text{Int } Y_0$ satisfying $\Lambda(t)(\Delta_2) = \Delta_2$, and at least one positive steady state (S_3, I_3, C_3) .

The following result on E_4 is derived directly from Lemma 3.11.

Theorem 3.12 Model (2.5) has at least one endemic steady state without zooplankton E_3 if $R_p > 1$ and $R_0 > 1$.

- **Remark 3.13** 1. From Theorem 3.12, chytrids cannot spread between phytoplankton if $R_0 < 1$ and can be prevalent if $R_0 > 1$. We do not obtain the results for the uniqueness and stability of E_3 . It is a question that deserves further exploration. It can be seen from numerical simulations that a spatially inhomogeneous periodic solution in the (S, I, C) quadrant is generated if E_3 is unstable (see Fig. 4).
- 2. Note that the movements of both phytoplankton and free-living chytrid zoospores are driven by the turbulence. It is very reasonable to assume that $d_p = d_c$. By Fig. 5a and b, R_0 is increasing and then decreasing for the spatial factors $d_p(d_c)$ and v. This shows that lower or higher turbulence intensities (sinking velocity) are both beneficial to controlling chytrid infection of phytoplankton. R_0 is strictly monotonically increasing for θ and q (see Fig. 5c and d). Hence the increase in θ and q is conducive to chytrid transmission among phytoplankton.

We next explore the endemic steady state with zooplankton E_4 . We introduce projections $Q_i : C([0, x_h], \mathbb{R}^2_+) \to C([0, x_h], \mathbb{R}_+), i = 1, 2$ as

$$Q_1(S, Z) = S, \ Q_2(S, Z) = Z$$

and $P_j : C([0, x_h], \mathbb{R}^3_+) \to C([0, x_h], \mathbb{R}_+), j = 1, 2, 3$ by

$$P_1(S, I, C) = S, P_2(S, I, C) = I, P_3(S, I, C) = C.$$

Let

$$\Theta_i = Q_i(\Delta_1), \ i = 1, 2, \ \Pi_j = P_j(\Delta_2), \ j = 1, 2, 3.$$



Fig. 4 The spatially inhomogeneous boundary periodic solution for the phytoplankton-chytrid coexistence. Here $d_p = d_c = d_z = 0.2$, v = 0.2, $m_z = 0.6$

Denote

$$S_*(x) = \inf_{S \in \Theta_1} S(x), \ S^*(x) = \sup_{S \in \Theta_1} S(x), \ Z^*(x) = \sup_{Z \in \Theta_2} Z(x) \text{ on } [0, x_h]$$

and

$$\underline{S} = \inf_{S \in \Pi_1} S(x), \ \underline{I} = \inf_{I \in \Pi_2} I(x), \ \underline{C} = \inf_{C \in \Pi_3} C(x) \text{ on } [0, x_h].$$

It follows from Lemmas 3.8 and 3.11 that

$$0 < S_*(x) \le S^*(x), \ 0 < Z^*(x), \ 0 < \underline{S}(x), \underline{I}(x), \underline{C}(x) \text{ on } [0, x_h].$$

We consider the linear parabolic system

$$\begin{split} \hat{I}_t &= d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} l_1 C - (m_p + \omega + \beta l_3) \hat{I}, \ x \in (0, x_h), \ t > 0, \\ C_t &= d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - (m_c + \theta l_2 + \gamma l_3) C, \ x \in (0, x_h), \ t > 0, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > 0 \end{split}$$

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Fig. 5 Dependence of R_0 on the spatial factors d_p , d_c , v and infection-related factors θ , q. Here $\mathbf{a} \theta = 7.5 \times 10^{-6} \mathbf{b} d_p = d_c = 0.5$, $\theta = 7 \times 10^{-6} \mathbf{c} d_p = d_c = 0.5 \mathbf{d} d_p = d_c = 0.5$, $\theta = 7.5 \times 10^{-6}$

for $l_i \in C([0, x_h], \mathbb{R}_+)$, i = 1, 2, 3. Replacing $m_p + \omega$, $m_c + \theta l_2$ by $m_p + \omega + \beta l_3$, $m_c + \theta l_2 + \gamma l_3$ in (3.13) and (3.15) respectively, we let $\Pi^{(l_2, l_3)}(t) : C([0, x_h], \mathbb{R}^2) \rightarrow C([0, x_h], \mathbb{R}^2)$ be the solution semigroup of (3.13) and let $\lambda_1(l_1, l_2, l_3)$ be principal eigenvalue of (3.15). Define the basic reproduction number associated with (l_1, l_2, l_3) by

$$R_0(l_1, l_2, l_3) = r(H^{(l_1, l_2, l_3)})$$

Here $r(H^{(l_1,l_2,l_3)})$ is the spectral radius and

$$H^{(l_1,l_2,l_3)}(\zeta_1,\zeta_2)(x) = \int_0^\infty \mathcal{F}^{l_1}(x)\Pi^{(l_2,l_3)}(t)(\zeta_1(x),\zeta_2(x))dt,$$

where \mathcal{F}^{l_1} can been found in (3.14). Applying Theorem 3.1 (i) in Wang and Zhao (2012) again, $\lambda_1(l_1, l_2, l_3)$ and $R_0(l_1, l_2, l_3) - 1$ have the same sign.

Let

$$X_0 := \{ (S, I, C, Z) \in X : S(\cdot) \neq 0, I(\cdot) \neq 0, C(\cdot) \neq 0, Z(\cdot) \neq 0 \}, \ \partial X_0 = X \setminus X_0.$$

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It follows that $\Psi(t) : X_0 \to X_0$ for all $t \ge 0$, where Ψ can been found in (3.7). From Theorem 3.1 and Remark 3.2, $\Psi(t)$ is compact for any t > 0 and has a global compact attractor in X. Assume that

$$\Omega_1 := \{ (S, 0, 0, Z) \in X : (S, Z) \in \Delta_1 \}, \ \Omega_2 := \{ (S, I, C, 0) \in X : (S, I, C) \in \Delta_2 \}.$$

It will be shown that E_0 , E_1 , Ω_1 , Ω_2 are uniform weak repellers for X_0 , that is, there exist σ_i , i = 1, 2, 3, 4 satisfying

 $\lim_{t \to \infty} \sup \operatorname{dist}(\Psi(t)u_0, E_0) \ge \sigma_1, \quad \limsup_{t \to \infty} \operatorname{dist}(\Psi(t)u_0, E_1) \ge \sigma_2,$ $\lim_{t \to \infty} \sup \operatorname{dist}(\Psi(t)u_0, \Omega_1) \ge \sigma_3, \quad \limsup_{t \to \infty} \operatorname{dist}(\Phi(t)u_0, \Omega_2) \ge \sigma_4$

for all $u_0 = (S_0, I_0, C_0, Z_0) \in X_0$. This proof of the following lemma is provided in Appendix.

Lemma 3.14 (i) E_0 is a uniform weak repeller for X_0 if $R_p > 1$, and E_1 is a uniform weak repeller for X_0 if $R_z > 1$; (ii) Ω_1 is a uniform weak repeller for X_0 if $R_0(S_*, S^*, Z^*) > 1$, and Ω_2 is a uniform weak repeller for X_0 if

$$\underline{R}_{z}(\underline{S},\underline{I},\underline{C}) = \frac{\lambda_{1}(d_{z},e_{p}(\alpha\underline{S}+\beta\underline{I})+e_{c}\gamma\underline{C})}{m_{z}} > 1.$$

The uniform persistence of (2.5) and the existence of E_4 are stated in the following conclusion.

Theorem 3.15 If $R_p > 1$, $R_z > 1$, $R_0(S_*, S^*, Z^*) > 1$, $\underline{R}_z(\underline{S}, \underline{I}, \underline{C}) > 1$, then model (2.5) is uniformly persistent for $(X_0, \partial X_0)$. Furthermore, model (2.5) has at least one endemic steady state with zooplankton E_4 .

Proof Let $\Gamma := \{u_0 \in \partial X_0 : \Psi(t)u_0 \in \partial X_0 \text{ for any } t \ge 0\}$ and the orbit $o(u_0) := \{\Psi(t)u_0 : u_0 \in \Gamma, t \ge 0\}$. It will prove that the omega limit set $\omega(u_0) \subset E_0 \cup E_1 \cup \Omega_1 \cup \Omega_2 \text{ of } o(u_0)$. For any $u_0 \in \Gamma$, from the definition of Γ , we have $S(\cdot, t, u_0) \equiv 0$ or $I(\cdot, t, u_0) \equiv 0$, $C(\cdot, t, u_0) \equiv 0$ or $Z(\cdot, t, u_0) \equiv 0$ for all $t \ge 0$. Similar to the proof of Lemma 3.11, if $S(\cdot, t, u_0) \equiv 0$ or $I(\cdot, t, u_0) \equiv 0$, $C(\cdot, t, u_0) \equiv 0$, $Z(\cdot, t, u_0) \equiv 0$, then $\omega(u_0) \subset E_0 \cup E_1$. If $I(\cdot, t, u_0) \equiv 0$, $C(\cdot, t, u_0) \equiv 0$, then (2.5) simplifies to (3.18). It follows from Lemma 3.8 that $\omega(u_0) \subset \Omega_1$. If $Z(\cdot, t, u_0) \equiv 0$, then (2.5) reduces to (3.19), and $\omega(u_0) \subset \Omega_2$ from Lemma 3.11.

It follows from Lemma 3.14 that $E_0, E_1, \Omega_1, \Omega_2$ are uniform weak repellers for X_0 . To obtain our conclusion, we denote $\mathcal{G} : X \to [0, \infty)$ satisfying

$$\mathcal{G}(u_0) := \min\left\{\min_{x \in [0, x_h]} S_0(x), \min_{x \in [0, x_h]} I_0(x), \min_{x \in [0, x_h]} C_0(x), \min_{x \in [0, x_h]} Z_0(x)\right\}.$$

From $\Psi(t)(X_0) \subseteq X_0$, $\mathcal{G}^{-1}(0, \infty) \subseteq X_0$ and $\mathcal{G}(\Psi(t)u_0) > 0$ for any t > 0 if $\mathcal{G}(u_0) > 0$ or $u_0 \in X_0$ with $\mathcal{G}(u_0) = 0$. It follows that \mathcal{G} is a generalized distance function for Ψ .

In the light of the above analysis, $\omega(u_0) \subset E_0 \cup E_1 \cup \Omega_1 \cup \Omega_2$ for any $u_0 \in \Gamma$. This shows that $\Psi(t)(u_0) \to E_0$ or $\Psi(t)(u_0) \to E_1$ or $\Psi(t)(u_0) \to \Omega_1$ or $\Psi(t)(u_0) \to \Omega_2$ for $u_0 \in \partial X_0$ as $t \to \infty$, and then no subset of $\{E_0, E_1, \Omega_1, \Omega_2\}$ forms a cycle in ∂X_0 . $E_0, E_1, \Omega_1, \Omega_2$ are all isolated in X and $W_i^s \cap \mathcal{G}^{-1}(0, \infty) = \emptyset$, i = 1, 2, 3, 4since $E_0, E_1, \Omega_1, \Omega_2$ are uniform weak repellers for X_0 , where W_i^s , i = 1, 2, 3, 4are the stable sets of $E_0, E_1, \Omega_1, \Omega_2$ respectively. By Theorem 3 in Smith and Zhao (2001), $\min_{u \in \omega(u_0)} \mathcal{G}(u) > \varpi$ for any $u_0 \in X_0$ and some $\varpi > 0$. This shows that the uniform persistence is valid.

Following Theorem 3.7 and Remark 3.10 in Magal and Zhao (2005), $\Psi(t)$ admits a global attractor in X_0 . Applying Theorem 4.7 in Magal and Zhao (2005), model (2.5) has one endemic steady state with zooplankton $E_4 \in X_0$. From (3.9), we have

$$\begin{split} &-d_p S_4'' + v S_4' + (\eta (S_4 + I_4) + \theta C_4 + \alpha Z_4) S_4 = (r_p - m_p) S_4 \ge 0, \ x \in (0, x_h), \\ &-d_p I_4'' + v I_4' + (m_p + \omega + \beta Z_4) I_4 = \theta S_4 C_4 \ge 0, \ x \in (0, x_h), \\ &-d_c C_4'' + (m_c + \theta S_4 + \gamma Z_4) C_4 = q \omega I_4 \ge 0, \ x \in (0, x_h), \\ &-d_z Z_4'' + m_z Z_4 = (e_p (\alpha S_4 + \beta I_4) + e_c \gamma C_4) Z_4, \ x \in (0, x_h), \\ &d_p S_4'(0) - v S_4(0) = d_p S_4'(x_h) - v S_4(x_h) = 0, \\ &d_p I_4'(0) - v I_4(0) = d_p I_4'(x_h) - v I_4(x_h) = 0, \\ &C_4'(0) = C_4'(x_h) = Z_4'(0) = Z_4'(x_h) = 0. \end{split}$$

This means that $S_4(x) > 0$, $I_4(x) > 0$, $C_4(x) > 0$, $Z_4(x) > 0$ on $[0, x_h]$ by applying the strong maximum principle and the Hopf boundary lemma.

- **Remark 3.16** 1. From Lemmas 3.8 and 3.11, $R_0(S_*, S^*, Z^*) = R_0(S_2, S_2, Z_2)$ if $\Delta_1 = (S_2, Z_2)$ and $\underline{R}_z(\underline{S}, \underline{I}, \underline{C}) = \underline{R}_z(S_3, I_3, C_3)$ if $\Delta_2 = (S_3, I_3, C_3)$. It is very difficult to compare the values of R_0 and $R_0(S_*, S^*, Z^*)$ or R_z and $\underline{R}_z(\underline{S}, \underline{I}, \underline{C})$. This means that in the mycoloop, it is not possible to distinguish whether zooplankton are more likely to invade aquatic ecosystems or chytrids are more prone to spread between phytoplankton.
- It follows from uniform persistence that phytoplankton, chytrids and zooplankton can coexist in a poorly mixed aquatic environment. There are two forms of coexistence. One is a steady state solution from Theorem 3.15. The other is a positive spatially inhomogeneous periodic solution from numerical analysis (see Fig. 6).

4 Mycoloop

The mycoloop contains multiple predation terms and one chytrid transmission. This complex structure has important implications for aquatic ecosystems (Frenken et al. 2020a, b; Kagami et al. 2014). We will explore the effects of some ecological factors on the mycoloop based on model (2.5). In this process, it also will reveal the roles of the mycoloop on phytoplankton blooms and chytrid transmission. The numerical algorithm in the figures below is performed in Matlab by discretizing model (2.5) via the finite difference method (see Appendix B in Zhang et al. (2021a)). The parameter





Fig. 6 The positive spatially inhomogeneous periodic solution for the Phytoplankton-chytrid-zooplankton coexistence. Here $d_p = d_c = d_z = 0.2$

values here come from Table 1. The initial values of the solutions are $S_0(x) = 40 + 5 \sin x$, $I_0(x) = 20 + 5 \cos x$, $C_0(x) = 30 + 10 \cos x$ and $Z_0(x) = 20 + 10 \sin x$ on $[0, x_h]$.

We consider the parameters in model (2.5) associated with ecological factors. These parameters involve spatial factors d_p , d_c , d_z , v, infection-related factor θ , zooplankton invasion-related factor m_z . The numerical bifurcation diagrams below exhibit the evolution trend of steady state solutions (E_i , i = 0, 1, 2, 3, 4) or spatially inhomogeneous periodic solutions with different parameter values. The points on the bifurcation curves represent the total biomass densities in space of susceptible phytoplankton ($\int_0^{x_h} S(x)dx$), infected phytoplankton ($\int_0^{x_h} I(x)dx$), free-living chytrid zoospores ($\int_0^{x_h} C(x)dx$) and zooplankton ($\int_0^{x_h} Z(x)dx$) when the solutions of model (2.5) converge to different steady state solutions or spatially inhomogeneous periodic solutions. Time series diagrams show changes in the density of phytoplankton ($\int_0^{x_h} (S+I)(x, t)dx$), chytrids ($\int_0^{x_h} C(x, t)dx$) and zooplankton ($\int_0^{x_h} Z(x, t)dx$) over time.

The spatial distribution of plankton is mainly influenced by the turbulence in the water. This is because plankton either lack swimming ability or have very weak swimming ability (Huber et al. 2011; Huisman et al. 2006; Klausmeier and Litchman 2001; Tao et al. 2021). For simplicity, it can be assumed that $D = d_p = d_c = d_z$. Figure 7



Fig. 7 Bifurcation diagrams for the vertical turbulent diffusion coefficient $D \in [0.1, 2]$ ($D = d_p = d_c = d_z$). Here it describes the effects of D on the mycoloop, and v = 0, 2



Fig.8 Bifurcation diagrams for the sinking or buoyant velocity $v \in [-0.2, 0.6]$. Here it describes the effects of v on the mycoloop

displays the effects of D on the mycoloop. All populations in the mycoloop coexist at the steady state solution E_4 as the value of D approaches 0.1. With the increase of D, positive spatially inhomogeneous periodic solutions through a Hopf bifurcation are generated, and the variation of their amplitudes is non-monotonic with respect to D. When D is relatively large, the biomass of zooplankton decreases dramatically and becomes extinct. At this point the mycoloop disappears and only phytoplankton and chytrids coexist. This occurs because the movement of plankton is controlled by the turbulence, then the faster diffusion rate is unfavorable for zooplankton to capture prey. These studies indicate that changes in the turbulence intensity cause more complex dynamics within the mycoloop and even disrupt the mycoloop structure.

The directional movement of phytoplankton consists of sinking (v > 0) and rising (v < 0) (Grover 2017; Zhang et al. 2021a). From Fig. 8, it can be seen that there are three different scenarios for varying values of v. The first is phytoplankton, chytrids and zooplankton coexist at periodic oscillations for $v \in (-0.2, -0.03) \cup (0.03, 0.48)$. The second is all populations coexist at E_4 for $v \in (0.48, 0.6)$. The third is the extinction of zooplankton and the destruction of the mycoloop for $v \in (-0.03, 0.03)$. This implies that if phytoplankton have no directional movement or the directional movement rate is low, it is not conducive to the mycoloop formation.

We next explore the parameter θ related to chytrid transmission. By Fig. 9, one can observe that there are three distinct stages with the increase of θ . For $\theta \in (10^{-4}, 1.5 \times 10^{-4})$, E_2 is globally attractive. This means that only phytoplankton and zooplankton coexist and chytrids cannot spread among phytoplankton if the infection rate is relatively low. For $\theta \in (1.5 \times 10^{-4}, 5.5 \times 10^{-4})$, chytrids spread among phytoplankton and the mycoloop induced by chytrids appears. All populations coexist at E_4 or a positive periodic solution. The spatially inhomogeneous periodic solutions bifurcate from E_4 at $\theta = 3.6 \times 10^{-4}$ via a Hopf bifurcation. For $\theta \in (5.5 \times 10^{-4}, 8 \times 10^{-4})$, zooplankton tend to extinction, and the mycoloop is destroyed. The reason for this phenomenon is that high infection rate reduces the number of free-living chytrid zoospores



Fig. 9 Bifurcation diagrams for the infection rate $\theta \in [10^{-4}, 8 \times 10^{-4}]$. Here it describes the effects of θ on the mycoloop



Fig. 10 Bifurcation diagrams for the loss rate $m_z \in [0.2, 1.8]$. Here it describes the effects of m_z on the mycoloop, and $\theta = 5 \times 10^{-5}$

in the water, resulting in the inability of the zooplankton to survive. The above discussion shows that a low infection rate reduces the probability of chytrid transmission among phytoplankton, and a high infection rate prevents zooplankton invasion.

Zooplankton are the only consumer within the mycoloop. Figure 10 shows the effects of changes in zooplankton biomass on the mycoloop. When zooplankton go extinct ($m_z > 1.56$), the steady state solution E_3 is globally attractive and chytrids are prevalent among phytoplankton. Zooplankton successfully invade aquatic ecosystems at $m_z = 1.56$. With further reductions in zooplankton mortality, the biomass of both infected phytoplankton and free-living chytrid zoospores declines. Chytrids are unable to spread among phytoplankton and E_2 is globally attractive if the zooplankton biomass is high ($m_z < 0.28$). These findings suggest that zooplankton can effectively control chytrid transmission among phytoplankton by consuming free-living chytrid zoospores.

Phytoplankton blooms are becoming more frequent and seriously threatening aquatic ecosystems (Chen et al. 2015; Ho et al. 2019). It describes an ecological phenomenon in which phytoplankton biomass increases dramatically. Zooplankton and chytrids can control phytoplankton biomass through predation or infection respectively (see Figs. 11a and 12a). Due to the complex relationship between phytoplankton, chytrids and zooplankton in the mycoloop, the phytoplankton biomass declines in the mycoloop (see Fig. 11b). This happens because phytoplankton infected with chytrids have a significant increase in mortality and become more easy to predation by zooplankton after fragmentation. In this way the spread of chytrids in the mycoloop together with zooplankton effectively suppresses the phytoplankton biomass. Another situation is that the presence of zooplankton in the mycoloop consumes a large number of free-living chytrid zoospores, thereby reducing chytrid transmission



Fig. 11 Time series of densities of phytoplankton, chytrids and zooplankton. Comparing **a** and **b**, the phytoplankton biomass declines in the mycoloop



Fig. 12 Time series of densities of phytoplankton, chytrids and zooplankton. Comparing **a** and **b**, the phytoplankton biomass increases in the mycoloop

among phytoplankton. Therefore, mycoloop can either control or induce phytoplankton blooms in different scenarios.

5 Discussion

Zooplankton consume both phytoplankton and free-living chytrid zoospores. Chytrids infect phytoplankton and fragment them for easy predation by zooplankton. The mycoloop describes the interactions of phytoplankton, chytrids and zooplankton (Frenken et al. 2020a, b; Miki et al. 2011). It enhances the sustainability and biodiversity of aquatic food webs (Kagami et al. 2014). There exist few mathematical models to consider the mycoloop. In order to better understand the mycoloop, it is reasonable to develop dynamic models to characterize the complex relationship between phytoplankton, chytrids and zooplankton.

The mycoloop model (2.5) in this study is proposed to characterize phytoplanktonchytrid-zooplankton interactions. The plankton habitat in a deep water column is poorly mixed vertically. Model (2.5) has two important features: one is to consider the mycoloop induced by chytrids, and the other is to contain spatial heterogeneity in the vertical direction. Theoretical and numerical outcomes show that the mycoloop model (2.5) with spatial heterogeneity has complicated dynamics and important ecological implications.

According to theorems in Sect. 3 and corresponding remarks, some critical thresholds for phytoplankton or zooplankton invasion and chytrid transmission among phytoplankton are rigorously derived. R_p , R_z , $\underline{R}_z(\underline{S}, \underline{I}, \underline{C})$ are the basic ecological reproductive indices for phytoplankton or zooplankton invasion (see Theorems 3.6, 3.9 and 3.15). R_0 , $R_0(S_*, S^*, Z^*)$ are the basic reproduction numbers for chytrid transmission among phytoplankton (see Theorems 3.12 and 3.15). Based on model (2.5) and numerical simulations, the effects of some ecological factors on the mycoloop are investigated. The numerical bifurcation diagrams (Figs. 7, 8, 9 and 10) show that spatial factors d_p , d_c , d_z , v, infection-related factor θ , and zooplankton invasion-related factor m_z induce more complex dynamics within the mycoloop and influence the formation and breakup of the mycoloop. The studies also indicate that the presence of zooplankton in the mycoloop can inhibit chytrid transmission among phytoplankton. Time series diagrams (Figs. 11 and 12) suggest that the mycoloop may either control or cause phytoplankton blooms.

Light is one of the essential resources for phytoplankton growth (Heggerud et al. 2023; Hsu and Lou 2010; Huisman and Weissing 1994; Peng and Zhao 2016). It should be noted that light has a significant effect on chytrid transmission among phytoplankton (Bruning 1991). In model (2.5), we do not consider the contribution of light. It is intriguing to incorporate light into the mycoloop. The paradox of the plankton refers to the contradiction between phytoplankton biodiversity in the same ecological niche and the limited availability of abiotic resources (Hutchinson 1961). Chytrids and zooplankton can infect and consume a variety of phytoplankton, respectively. Hence it is necessary to include two or more phytoplankton in the mycoloop and to attempt to explain the plankton paradox. Additionally, it may be helpful to investigate the influences of lake stratification and fish. We have made a preliminary discussion on dynamics of model (2.5), but there are still some remaining open problems to be explored, for instance, the existence of spatially inhomogeneous periodic solutions, the uniqueness and stability of E_3 , E_4 .

Appendix

Proof of Lemma 3.11 This proof mainly applies the abstract persistence theory in Li and Zhao (2021); Magal and Zhao (2005); Smith and Zhao (2001); Zhao (2017). It follows from the Hopf boundary lemma and the strong maximum principle that

$$S(x, t, u_0) > 0, \ I(x, t, u_0) > 0, \ C(x, t, u_0) > 0$$
 (A.1)

on $[0, x_h]$ for all t > 0 and any initial value $u_0 = (S_0, I_0, C_0) \in Y_0$, and then $\Lambda(t)Y_0 \subseteq Y_0$ for all $t \ge 0$. Let $\Upsilon := \{u_0 \in \partial Y_0 : \Lambda(t)u_0 \in \partial Y_0 \text{ for all } t \ge 0\}$ and the orbit $o(u_0) := \{\Lambda(t)u_0 : u_0 \in \Upsilon, t \ge 0\}$.

We claim that the omega limit set $\omega(u_0) = \{(0, 0, 0), (S_1, 0, 0)\}$ of $o(u_0)$. For any $u_0 \in \Upsilon$, we have $\Lambda(t)u_0 \in \Upsilon$, $t \ge 0$. This means that $S(\cdot, t, u_0) \equiv 0$ or $I(\cdot, t, u_0) \equiv 0, C(\cdot, t, u_0) \equiv 0$. If $S(\cdot, t, u_0) \equiv 0$, then (3.19) reduces to

$$I_t = d_p I_{xx} - v I_x - (m_p + \omega) I, \ x \in (0, x_h), \ t > 0,$$

$$C_t = d_c C_{xx} + q \omega I - m_c C, \ x \in (0, x_h), \ t > 0,$$

$$d_p I_x(0, t) - v I(0, t) = d_p I_x(x_h, t) - v I(x_h, t) = 0, \ t > 0.$$

$$C_x(0, t) = C_x(x_h, t) = 0, \ t > 0.$$

It follows that $\lim_{t\to\infty} I(\cdot, t, u_0) = 0$, $\lim_{t\to\infty} C(\cdot, t, u_0) = 0$. If $I(\cdot, t, u_0) \equiv 0$ and $C(\cdot, t, u_0) \equiv 0$, then (3.19) is transformed into (3.12), which implies that $\lim_{t\to\infty} S(x, t, u_0) = S_1(x)$ on $[0, x_h]$. Hence the claim is true.

We next prove that (0, 0, 0), $(S_1, 0, 0)$ are uniform weak repellers for Y_0 , that is, there exist $\delta_i > 0$, i = 0, 1 satisfying

$$\limsup_{t \to \infty} \|\Lambda(t)u_0 - (0, 0, 0)\| \ge \delta_0$$
(A.2)

$$\limsup_{t \to \infty} \|\Lambda(t)u_0 - (S_1, 0, 0)\| \ge \delta_1$$
(A.3)

for all $u_0 \in Y_0$. If (A.2) does not hold, then for any $\varepsilon_0 > 0$, there exist $u_0 \in Y_0$ and $t_0 > 0$ satisfying

$$||S(\cdot, t, u_0)|| < \varepsilon_0, ||I(\cdot, t, u_0)|| < \varepsilon_0, ||C(\cdot, t, u_0)|| < \varepsilon_0 \text{ for } t \ge t_0.$$

From the *S* equation in (3.19), we have

$$S_{t} \ge d_{p}S_{xx} - vS_{x} + (r_{p} - m_{p} - 2\eta\varepsilon_{0} - \theta\varepsilon_{0})S, \ x \in (0, x_{h}), \ t > t_{0},$$

$$d_{p}S_{x}(0, t) - vS(0, t) = d_{p}S_{x}(x_{h}, t) - vS(x_{h}, t) = 0, \ t > t_{0}.$$

Following the maximum principle, we obtain $S(\cdot, t_0, u_0) > 0$ for $u_0 \in Y_0$. Let $r_p - m_p - 2\eta\varepsilon_0 - \theta\varepsilon_0$ be the principal eigenvalue of (3.10) with $l(x) = r_p - m_p - 2\eta\varepsilon_0 - \theta\varepsilon_0$ and $d = d_p$, and let ϕ^{ε_0} be the corresponding positive eigenfunction. For the above sufficiently small $\varepsilon_0, r_p - m_p - 2\eta\varepsilon_0 - \theta\varepsilon_0 > 0$ since $R_p > 1$. We can find a $a_0 > 0$ satisfying $S(\cdot, t_0, u_0) \ge a_0 \phi^{\varepsilon_0}$. By the comparison theorem of parabolic system, we have

$$S(x,t) \ge a_0 e^{(r_p - m_p - 2\eta\varepsilon_0 - \theta\varepsilon_0)(t - t_0)} \phi^{\varepsilon_0}(x), \ x \in [0, x_h], \ t \ge t_0.$$

Here $a_0 e^{(r_p - m_p - 2\eta\varepsilon_0 - \theta\varepsilon_0)(t - t_0)} \phi^{\varepsilon_0}(x)$ is a solution of

$$S_t = d_p S_{xx} - v S_x + (r_p - m_p - 2\eta \varepsilon_0 - \theta \varepsilon_0) S, \ x \in (0, x_h), \ t > t_0,$$

$$d_p S_x(0, t) - v S(0, t) = d_p S_x(x_h, t) - v S(x_h, t) = 0, \ t > t_0,$$

$$S(x, t_0) = a_0 \phi^{\varepsilon_0}(x), \ x \in [0, x_h].$$

This implies that $\lim_{t\to\infty} S(\cdot, t, u_0) = \infty$ since $r_p - m_p - 2\eta\varepsilon_0 - \theta\varepsilon_0 > 0$. It is in contradiction with $||S(\cdot, t, u_0)|| < \varepsilon_0$ for $t \ge t_0$. Therefore, (0, 0, 0) is a uniform weak repeller and it is isolated in $C([0, x_h], \mathbb{R}^3_+)$.

Assume that (A.3) is not true. Then for any $\varepsilon_s > 0$, there exist $u_s \in Y_0$ and $t_s > 0$ satisfying

$$\|S(\cdot, t, u_s) - S_1(\cdot)\| < \varepsilon_s, \ \|I(\cdot, t, u_s)\| < \varepsilon_s, \ \|C(\cdot, t, u_s)\| < \varepsilon_s \text{ for } t \ge t_s.$$
(A.4)

By the *I* and *C* equations in (3.19), we let $\hat{I} = Ie^{-(v/d_p)x}$ and obtain

$$\begin{split} \hat{I}_t &\ge d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} (S_1 - \varepsilon_s) C - (m_p + \omega) \hat{I}, \ x \in (0, x_h), \ t > t_s, \\ C_t &\ge d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - (m_c + \theta(S_1 + \varepsilon_s)) C, \ x \in (0, x_h), \ t > t_s, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > t_s. \end{split}$$

From the maximum principle, we get $\hat{I}(\cdot, t_s, u_s) > 0$ and $C(\cdot, t_s, u_s) > 0$ for $u^s \in Y_0$. Denote $\lambda_1(S_1 - \varepsilon_s, S_1 + \varepsilon_s)$ be the principal eigenvalue of (3.15) with $l_1 = S_1 - \varepsilon_s$ and $l_2 = S_1 + \varepsilon_s$, and $(\varphi^{\varepsilon_s}, \psi^{\varepsilon_s})$ be the corresponding positive eigenfunction. For the sufficiently small $\varepsilon_s, \lambda_1(S_1 - \varepsilon_s, S_1 + \varepsilon_s) > 0$ since $R_0 > 1$. There is a $a_s > 0$ such that $(\hat{I}(\cdot, t_s, u_s), C(\cdot, t_s, u_s)) \ge a_s(\varphi^{\varepsilon_s}, \psi^{\varepsilon_s})$. Applying the comparison theorem again, we obtain

$$(\hat{I}(x,t,u_s), C(x,t,u_s)) \ge a_s e^{\lambda_1(S_1 - \varepsilon_s, S_1 + \varepsilon_s)(t - t_s)}(\varphi^{\varepsilon_s}, \psi^{\varepsilon_s}) \text{ for all } x \in [0, x_h], \ t \ge t_s.$$

Here $a_s e^{\lambda_1(S_1 - \varepsilon_s, S_1 + \varepsilon_s)(t - t_s)}(\varphi^{\varepsilon_s}, \psi^{\varepsilon_s})$ is a solution of

$$\begin{split} \hat{I}_{t} &= d_{p}\hat{I}_{xx} + v\hat{I}_{x} + \theta e^{-(v/d_{p})x}(S_{1} - \varepsilon_{s})C - (m_{p} + \omega)\hat{I}, \ x \in (0, x_{h}), \ t > t_{s}, \\ C_{t} &= d_{c}C_{xx} + q\omega e^{(v/d_{p})x}\hat{I} - (m_{c} + \theta(S_{1} + \varepsilon_{s}))C, \ x \in (0, x_{h}), \ t > t_{s}, \\ \hat{I}_{x}(0, t) &= \hat{I}_{x}(x_{h}, t) = C_{x}(0, t) = C_{x}(x_{h}, t) = 0, \ t > t_{s}, \\ (\hat{I}(x, t_{s}, u_{s}), C(x, t_{s}, u_{s})) = a_{s}(\varphi^{\varepsilon_{s}}, \psi^{\varepsilon_{s}}), \ x \in [0, x_{h}]. \end{split}$$

Then $\hat{I}(\cdot, t, u_s)$, $C(\cdot, t, u_s)$ are unbounded since $\lambda_1(S_1 - \varepsilon_s, S_1 + \varepsilon_s) > 0$. It contradicts (A.4). This indicates that $(S_1, 0, 0)$ is a uniform weak repeller and it is isolated in $C([0, x_h], \mathbb{R}^3_+)$.

To complete the proof, we denote $\mathcal{F}: C([0, x_h], \mathbb{R}^3_+) \to [0, \infty)$ satisfying

$$\mathcal{F}(u_0) := \min\left\{\min_{x \in [0, x_h]} S_0(x), \min_{x \in [0, x_h]} I_0(x), \min_{x \in [0, x_h]} C_0(x)\right\}$$

for any $u_0 = (S_0, I_0, C_0) \in C([0, x_h], \mathbb{R}^3_+)$. It follows from (A.1) that $\mathcal{F}^{-1}(0, \infty) \subseteq Y_0$ and $\mathcal{F}(\Lambda(t)u_0) > 0$ for any t > 0 if $\mathcal{F}(u_0) > 0$ or $u_0 \in Y_0$ with $\mathcal{F}(u_0) = 0$. Hence, \mathcal{F} is a generalized distance function for $\Lambda(t)$. From Theorem 3.1 and Remark 3.2, it is easy to see that $\Lambda(t)$ is compact for all t > 0

0 and has a global compact attractor in $C([0, x_h], \mathbb{R}^3_+)$. From $\bigcup_{u_0 \in \Upsilon} \omega(u_0) = \{(0, 0, 0), (S_1, 0, 0)\}$, we have $(S(\cdot, t, u_0), I(\cdot, t, u_0), C(\cdot, t, u_0)) \rightarrow (0, 0, 0)$ or $(S(\cdot, t, u_0), I(\cdot, t, u_0), C(\cdot, t, u_0)) \rightarrow (S_1, 0, 0)$ as $t \rightarrow \infty$. This implies that there is no cycle in ∂Y_0 for $\Lambda(t)$ from $\{(0, 0, 0)\} \cup \{(S_1, 0, 0)\}$ to $\{(0, 0, 0)\} \cup \{(S_1, 0, 0)\}$. Denote $W^s(\{(0, 0, 0)\})$ and $W^s(\{(S_1, 0, 0)\})$ as the stable sets of $\{(0, 0, 0)\}$ and $\{(S_1, 0, 0)\}$ respectively. Note that (0, 0, 0) and $(S_1, 0, 0)$ are uniform weak repellers. Thus, (0, 0, 0) and $(S_1, 0, 0)$ are isolated in $C([0, x_h], \mathbb{R}^3_+)$ and $W^s(\{(0, 0, 0)\}) \cap \mathcal{F}^{-1}(0, \infty) = \emptyset$. From Theorem 3 in Smith and Zhao (2001), $\min_{(S, I, C) \in \omega(u_0)} \mathcal{F}((S, I, C)) > \nu$ for any $u_0 \in Y_0$ and some $\nu > 0$. It follows that the uniform persistence holds.

It follows from Theorem 3.7 and Remark 3.10 in Magal and Zhao (2005) that $\Lambda(t) : Y_0 \to Y_0$ admits a global attractor $\Delta_2 \subset Y_0$ satisfying $\Lambda(t)(\Delta_2) = \Delta_2$. Moreover, $\Delta_2 \subset \text{Int } Y_0$ since (A.1) holds. By Theorem 4.7 in Magal and Zhao (2005), model (2.5) has a steady state $(S_3, I_3, C_3) \in Y_0$. By (3.8), we have

$$\begin{aligned} &-d_p S_3'' + v S_3' + \eta (S_3 + I_3) S_3 = (r_p - m_p) S_3 \ge 0, \ x \in (0, x_h), \\ &-d_p I_3'' + v I' + (m_p + \omega) I_3 = \theta S_3 C_3 \ge 0, \ x \in (0, x_h), \\ &-d_c C_3'' + (m_c + \theta S_3) C_3 = q \omega I_3 \ge 0, \ x \in (0, x_h), \\ &d_p S_3'(0) - v S_3(0) = d_p S_3'(x_h) - v S_3(x_h) = 0, \\ &d_p I_3'(0) - v I_3(0) = d_p I_3'(x_h) - v I_3(x_h) = 0, \\ &C_3'(0) = C_3'(x_h) = 0. \end{aligned}$$

Therefore, $S_3(x) > 0$, $I_3(x) > 0$ and $C_3(x) > 0$ on $[0, x_h]$ by applying the strong maximum principle and the Hopf boundary lemma.

Proof of Lemma 3.14 (i) Similar to the one in Lemma 3.11, E_0 is a uniform weak repeller for X_0 by replacing $r_p/(m_p + 2\eta\varepsilon_0 + \theta\varepsilon_0)$ with $r_p/(m_p + 2\eta\varepsilon_0 + \theta\varepsilon_0 + \alpha\varepsilon_0)$. If E_1 is not a uniform weak repeller, then for any $\varepsilon_1 > 0$, there exist $u_1 \in X_0$ and $\bar{t}_1 > 0$ satisfying

$$\|S(\cdot, t, u_1) - S_1(\cdot)\| < \varepsilon_1, \ \|I(\cdot, t, u_1)\| < \varepsilon_1, \ \|C(\cdot, t, u_1)\| < \varepsilon_1, \ \|Z(\cdot, t, u_1)\| < \varepsilon_1$$
(A.5)

for any $t \ge \overline{t_1}$. By the Z equation in (2.5), we get

$$Z_t \ge d_z Z_{xx} + (e_p \alpha (S_1 - \varepsilon_1) - m_z) Z, \ x \in (0, x_h), \ t > \bar{t}_1,$$

$$Z_x(0, t) = Z_x(x_h, t) = 0, \ t > \bar{t}_1.$$

Note that $Z(\cdot, \bar{t}_1, u_1) > 0$ for $u_0 \in Y_0$. Hence we can find a $a_1 > 0$ such that $Z(\cdot, \bar{t}_1, u_1) \ge a_1 \xi^{\varepsilon_1}$, where ξ^{ε_1} is the positive eigenfunction for $\lambda_1(d_z, e_p \alpha(S_1 - \varepsilon_1) - m_z)$. Hence we have

$$Z(x,t) \ge a_1 e^{\lambda_1 (d_z, e_p \alpha(S_1 - \varepsilon_1) - m_z)(t - \bar{t}_1)} \xi^{\varepsilon_1}(x), \ x \in [0, x_h], \ t \ge \bar{t}_1.$$

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$$Z_{t} = d_{z}Z_{xx} + (e_{p}\alpha(S_{1} - \varepsilon_{1}) - m_{z})Z, \ x \in (0, x_{h}), \ t > \bar{t}_{1},$$

$$Z_{x}(0, t) = Z_{x}(x_{h}, t) = 0, \ t > \bar{t}_{1},$$

$$Z(x, \bar{t}_{1}, u_{1}) = a_{1}\xi^{\varepsilon_{1}}, \ x \in [0, x_{h}].$$

For the above sufficiently small ε_1 , we have $\lambda_1(d_z, e_p \alpha(S_1 - \varepsilon_1) - m_z) > 0$ since $R_z > 1$. It follows that $\lim_{t\to\infty} Z(\cdot, t, u_1) = \infty$, which contradicts (A.5). This shows that (i) holds.

(ii) Assume that Ω_1 is not a uniform weak repeller for X_0 . For any $\varepsilon_2 > 0$, there exist $u_2 \in X_0$ and $\overline{t}_2 > 0$ satisfying

$$dist(S(\cdot, t, u_2), \Theta_1) < \varepsilon_2, \|I(\cdot, t, u_2)\| < \varepsilon_2, \|C(\cdot, t, u_2)\| < \varepsilon_2, dist(Z(\cdot, t, u_2), \Theta_2) < \varepsilon_2$$
(A.6)

for any $t \ge \overline{t_2}$. Note that Θ_i , i = 1, 2 are compact. There are $\hat{S}^t \in \Theta_1$ and $\hat{Z}^t \in \Theta_2$ such that

$$\|S(\cdot, t, u_2) - \hat{S}^t(\cdot)\| < \varepsilon_2, \ \|Z(\cdot, t, u_2) - \hat{Z}^t(\cdot)\| < \varepsilon_2 \text{ for } t \ge \bar{t}_2.$$

It follows that

$$S_*(\cdot) - \varepsilon_2 \le \hat{S}^t(\cdot) - \varepsilon_2 < S(\cdot, t, u_2) < \hat{S}^t(\cdot) + \varepsilon_2 \le S^*(\cdot) + \varepsilon_2,$$

$$Z(\cdot, t, u_2) < \hat{Z}^t(\cdot) + \varepsilon_2 \le Z^*(\cdot) + \varepsilon_2$$

for any $t \ge \overline{t}_2$. From the *I* and *C* equations in (2.5), we set $\hat{I} = Ie^{-(v/d_p)x}$ and have

$$\begin{split} \hat{I}_t &\ge d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} (S_* - \varepsilon_2) C - (m_p + \omega + \beta (Z^* + \varepsilon_2)) \hat{I}, \ x \in (0, x_h), \ t > \bar{t}_2, \\ C_t &\ge d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - (m_c + \theta (S^* + \varepsilon_2) + \gamma (Z^* + \varepsilon_2)) C, \ x \in (0, x_h), \ t > \bar{t}_2, \\ \hat{I}_x(0, t) &= \hat{I}_x(x_h, t) = C_x(0, t) = C_x(x_h, t) = 0, \ t > \bar{t}_2. \end{split}$$

Note that $\hat{I}(\cdot, \bar{t}_2, u_2) > 0$ and $C(\cdot, \bar{t}_2, u_2) > 0$ for $u_2 \in Y_0$. We can find a $a_2 > 0$ such that $(\hat{I}(\cdot, \bar{t}_2, u_2), C(\cdot, \bar{t}_2, u_2)) \ge a_2(\varphi^{\varepsilon_2}, \psi^{\varepsilon_2})$, where $(\varphi^{\varepsilon_2}, \psi^{\varepsilon_2})$ is the positive eigenfunction for $\lambda_1(S_* - \varepsilon_2, S^* + \varepsilon_2, Z^* + \varepsilon_2)$. For the sufficiently small $\varepsilon_2, \lambda_1(S_* - \varepsilon_2, S^* + \varepsilon_2, Z^* + \varepsilon_2) > 0$ since $R_0(S_*, S^*, Z^*) > 1$. It follows that

$$\left(\hat{I}(x,t,u_2), C(x,t,u_2)\right) \ge a_2 e^{\lambda_1 \left(S_* - \varepsilon_2, S^* + \varepsilon_2, Z^* + \varepsilon_2\right) \left(t - \overline{t_2}\right)} \left(\varphi^{\varepsilon_2}, \psi^{\varepsilon_2}\right) \text{ for all } x \in [0, x_h], \ t \ge \overline{t_2}.$$

Here $a_2 e^{\lambda_1(S_*-\varepsilon_2,S^*+\varepsilon_2,Z^*+\varepsilon_2)(t-\overline{t}_2)}(\varphi^{\varepsilon_2},\psi^{\varepsilon_2})$ is a solution of

$$\begin{split} \hat{I}_t &= d_p \hat{I}_{xx} + v \hat{I}_x + \theta e^{-(v/d_p)x} (S_* - \varepsilon_2) C - \left(m_p + \omega + \beta (Z^* + \varepsilon_2) \right) \hat{I}, \; x \in (0, x_h), \; t > \bar{t}_2, \\ C_t &= d_c C_{xx} + q \omega e^{(v/d_p)x} \hat{I} - \left(m_c + \theta (S^* + \varepsilon_2) + \gamma (Z^* + \varepsilon_2) \right) C, \; x \in (0, x_h), \; t > \bar{t}_2, \end{split}$$

Deringer

$$\begin{split} \bar{I}_x(0,t) &= \bar{I}_x(x_h,t) = C_x(0,t) = C_x(x_h,t) = 0, \ t > \bar{t}_2, \\ (\hat{I}\left(x,\bar{t}_2,u_2\right), C(x,\bar{t}_2,u_2)\right) &= a_2(\varphi^{\varepsilon_2},\psi^{\varepsilon_2}), \ x \in [0,x_h]. \end{split}$$

This indicates that $\hat{I}(\cdot, t, u_2)$, $C(\cdot, t, u_2)$ are unbounded since $\lambda_1(S_* - \varepsilon_2, S^* + \varepsilon_2, Z^* + \varepsilon_2) > 0$. This contradicts (A.6).

If Ω_2 is not a uniform weak repeller for X_0 , then for any $\varepsilon_3 > 0$, there exist $u_3 \in X_0$ and $\overline{t}_3 > 0$ satisfying

$$dist(S(\cdot, t, u_3), \Pi_1) < \varepsilon_3, \quad dist(I(\cdot, t, u_3), \Pi_2) < \varepsilon_3, dist(C(\cdot, t, u_3), \Pi_3) < \varepsilon_3, \quad \|Z(\cdot, t, u_3)\| < \varepsilon_3$$
(A.7)

for any $t \ge \bar{t}_3$. Since Π_j , j = 1, 2, 3 are compact, there are $\bar{S}^t \in \Pi_1$, $\bar{I}^t \in \Pi_2$ and $\bar{C}^t \in \Pi_3$ such that

$$\|S(\cdot,t,u_3)-\bar{S}^t(\cdot)\|<\varepsilon_3,\ \|I(\cdot,t,u_3)-\bar{I}^t(\cdot)\|<\varepsilon_3,\ \|C(\cdot,t,u_3)-\bar{C}^t(\cdot)\|<\varepsilon_3$$

for all $t \geq \overline{t_3}$. Hence,

$$\underline{S} - \varepsilon_3 \leq \overline{S}^t(\cdot) - \varepsilon_3 < S(\cdot, t, u_3),$$

$$\underline{I} - \varepsilon_3 \leq \overline{I}^t(\cdot) - \varepsilon_3 < I(\cdot, t, u_3),$$

$$C - \varepsilon_3 < \overline{C}^t(\cdot) - \varepsilon_3 < C(\cdot, t, u_3)$$

for any $t \geq \overline{t}_3$. Then

$$Z_t \ge d_z Z_{xx} + (e_p(\alpha(\underline{S} - \varepsilon_3) + \beta(\underline{I} - \varepsilon_3)) + e_c \gamma(\underline{C} - \varepsilon_3) - m_z)Z, \ x \in (0, x_h), \ t > \overline{t}_3,$$

$$Z_x(0, t) = Z_x(x_h, t) = 0, \ t > \overline{t}_3.$$

For the above sufficiently small $\varepsilon_3 > 0$, $\lambda_1(d_z, e_p(\alpha(\underline{S} - \varepsilon_3) + \beta(\underline{I} - \varepsilon_3)) + e_c \gamma(\underline{C} - \varepsilon_3) - m_z) > 0$ since $\underline{R}_z(\underline{S}, \underline{I}, \underline{C}) > 1$. Carrying out similar arguments as those in (i), we have $\lim_{t\to\infty} Z(\cdot, t, u_3) = \infty$. It is contradicted by (A.7). Therefore, (ii) holds. \Box

Data availability This manuscript does not include any direct data although most parameter values and units were obtained from the literature.

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