Mathematical Biosciences 387 (2025) 109507

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs

Original Research Article

Flow-driven dynamics in a mussel-algae system with nonlinear boundary interactions

Chaochao Li [a], Hao Wang [b], Shangjiang Guo [c,d,*]

[a] School of Statistics and Mathematics, Hubei University of Economics, Wuhan, Hubei 430205, PR China
[b] Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada
[c] School of Mathematics and Physics, China University of Geosciences, Wuhan, Hubei 430074, PR China
[d] Center for Mathematical Sciences, China University of Geosciences, Wuhan, Hubei 430074, PR China

ARTICLE INFO

Keywords:
Reaction–diffusion–advection system
Nonlinear boundary conditions
Persistence thresholds
Consumer-resource dynamics
Spatial ecology
Global dynamics

ABSTRACT

We investigate a reaction–diffusion–advection mussel-algae model with nonlinear boundary conditions, motivated by population dynamics in flowing aquatic environments. The system exhibits complex threshold behavior governed by energy conversion efficiency, flow velocity, and boundary-mediated losses. We establish conditions for global existence, boundedness, and characterize semi-trivial and coexistence steady states. By employing techniques compatible with the maximum principle under the structural assumption (H1) on the nonlinear boundary flux, along with super- and sub-solution methods, we rigorously analyze the persistence and extinction regimes. Our analysis reveal critical thresholds and bifurcations that determine species survival, with advection and nonlinear boundaries interacting to shape system dynamics. These findings generalize classical constant-flux models and offer a new framework for studying stability and bifurcation phenomena in reaction–advection–diffusion systems with biologically motivated boundary interactions.

1. Introduction

Aquatic ecosystems pose a fundamental survival challenge: how do populations persist in environments where water flow continually displaces organisms downstream? From fast-flowing rivers to tidal zones, numerous species succeed despite inhabiting what ecologists term *advective environments*—habitats characterized by persistent unidirectional flow. This phenomenon raises a central ecological question: how can riverine populations maintain themselves against currents that, in theory, should transport them out of the habitat? This apparent contradiction, known as the *drift paradox* [1,2], is resolved through a delicate interplay between physical forces and biological adaptations. Pioneering work by Speirs and Gurney [3] demonstrated that random movement (diffusion) counteracts advective displacement, while local population growth (reaction) compensates for losses. Their mathematical framework revealed how the interaction between advection, diffusion, and reaction enables population persistence. Subsequent studies have extended this theory [4–6] by incorporating (a) nonlinear reaction terms to model density-dependent growth, (b) spatially heterogeneous diffusion coefficients reflecting habitat variability, and (c) boundary conditions that represent ecological barriers. Collectively, these works demonstrate how the coupling between transport processes and population dynamics governs stable spatial distributions, with broad implications for ecological management, species conservation, and invasion dynamics.

The balance between species in natural ecosystems involves complex interactions, ranging from competition to mutualism. These dynamics become even more intricate in flowing environments, such as rivers and streams, where unidirectional water movement imposes additional ecological constraints. Recent research [7–16] has extended classical Lotka–Volterra competition models by incorporating advection, representing flow-induced transport, and diffusion, describing random organismal movement. The coupling of these processes produces unexpected survival outcomes, often challenging classical predator–prey theory. Central questions arise: under what conditions can prey populations persist when facing both predation and downstream displacement? When can stable coexistence between predators and prey occur in advective systems? How do variations in species mobility and flow velocity reshape ecological equilibria? A pivotal study by Hilker and Lewis [17] demonstrated that advective environments can generate rich dynamical behaviors, including unexpected coexistence, competitive exclusion, and dominance reversals. More recently, significant attention has focused on invasion dynamics in predator–prey systems, with notable advances reported in [18–23] and related works.

---

[*] Corresponding author at: School of Mathematics and Physics, China University of Geosciences, Wuhan, Hubei 430074, PR China
E-mail address: guosj@cug.edu.cn (S. Guo).

https://doi.org/10.1016/j.mbs.2025.109507
Received 12 May 2025; Received in revised form 29 June 2025; Accepted 14 July 2025

In ecological modeling, a natural refinement for increasing biological realism is the incorporation of density dependence. Kuussaari et al. [24] observed the behavior of Glanville fritillary butterflies on their habitat patches. They found that the butterflies were less likely to leave a patch when conspecifics were present, and that populations within patches showed an Allee effect. Motivated by the observations of the ecologist Kuussaari and his collaborators [24] of Glanville fritillary butterflies on habitat patches, Cantrell et al. [25] observed that coefficients in reaction–diffusion models, including boundary conditions, may depend on population density, leading to systems with nonlinear boundary effects. Subsequently, Cantrell et al. [26] simulated a logistic model for the diffusion and growth of an organism population within a habitat patch, where the probability of individuals crossing the patch boundary and dispersing decreased with increasing local density. Their work [26] highlighted the importance of density-dependent behavior at habitat edges and its relation to the Allee effect. The existence, uniqueness, and stability of steady-state solutions for reaction–diffusion systems with nonlinear boundary conditions have been extensively studied [27–32], employing bifurcation theory and related analytical techniques.

In this paper, we analyze a spatially explicit consumer-resource system modeling the ecological interaction between stationary freshwater mussels and their drifting algal food source in a flowing aquatic environment. To better capture real-world riverine dynamics, we incorporate nonlinear boundary conditions that reflect biologically realistic processes:

$$\begin{cases} u_t = d_1 u_{xx} - q u_x + a(1-u) - uv, & 0<x<L,\ t>0, \\ v_t = d_2 v_{xx} + \gamma uv - \dfrac{v}{1+v}, & 0<x<L,\ t>0, \\ d_1 u_x(0,t) - qu(0,t) = 0, & t>0, \\ d_1 u_x(L,t) - qu(L,t) = u(L,t)g(u(L,t)), & t>0, \\ v_x(0,t) = v_x(L,t) = 0, & t>0, \\ u(x,0) = \varphi_1(x) \geq 0,\ \not\equiv 0, \quad v(x,0) = \varphi_2(x) \geq 0,\ \not\equiv 0, & 0 \leq x \leq L, \end{cases} \tag{1.1}$$

where $u(x,t)$ and $v(x,t)$ denote the densities of algae and mussels, respectively. The algal dynamics incorporate diffusion ($d_1 > 0$), downstream advection ($q \geq 0$), and vertical exchange or growth ($a > 0$), while mussels disperse locally through diffusion ($d_2 > 0$) with an energy conversion efficiency $\gamma > 0$. The boundary conditions encode key ecological constraints: (i) mussels satisfy homogeneous Neumann conditions ($v_x = 0$ at $x = 0, L$), representing a closed population; (ii) algae experience a no-flux condition upstream ($d_1 u_x = qu$ at $x = 0$), preventing escape at the domain entrance; and (iii) the downstream algal outflow flux depends nonlinearly on the local algal density at $x = L$ through a boundary function $g(u(L,t))$. This setting leads to a mathematically rich structure, where nonlinear boundary effects interact with internal reaction–advection–diffusion dynamics, significantly influencing the system's behavior. Model (1.1) was first introduced by Cangelosi et al. [33] who investigated the spatial distribution patterns of model (1.1) on an unbounded spatial domain in the absence of advection effects and nonlinear boundary conditions through weakly nonlinear diffusive instability analysis. We refer to [33, 34] for a complete model derivation and parameter interpretation.

Throughout this paper, we impose the following structural assumption on the boundary flux function:

(H1) The boundary loss term $g(u) \in C^{1+\delta}(\mathbb{R})$ with $\delta \in (0,1)$ satisfies $g(u) \leq 0$ for all $u \in \mathbb{R}$.

This condition serves three key mathematical purposes: first, the Hölder continuity ($C^{1+\delta}$) guarantees sufficient smoothness for existence and regularity theory; second, the non-positivity constraint ($-g(u) \geq 0$) corresponds biologically to the interpretation that boundary flux represents a loss (and never a gain) of algal population at $x = L$; third, the condition ensures that the maximum principle holds (Theorem 2.1), which is crucial for obtaining a priori estimates and preventing unphysical solutions. The term $-g(u)$ quantifies the population loss rate at the downstream boundary relative to the advective flow rate q, with larger values corresponding to greater boundary mortality effects. This formulation generalizes classical Robin boundary conditions while maintaining biological realism [12].

The degenerate case $g(u) \equiv 0$ reduces system (1.1) to classical no-flux boundary conditions, yielding the simplified mussel-algae model:

$$\begin{cases} u_t = d_1 u_{xx} - q u_x + a(1-u) - uv, & 0<x<L,\ t>0, \\ v_t = d_2 v_{xx} + \gamma uv - \dfrac{v}{1+v}, & 0<x<L,\ t>0, \\ d_1 u_x(0,t) - qu(0,t) = d_1 u_x(L,t) - qu(L,t) = 0, & t>0, \\ v_x(0,t) = v_x(L,t) = 0, & t>0, \\ u(x,0) = \varphi_1(x) \geq 0, \quad v(x,0) = \varphi_2(x) \geq 0, & 0 \leq x \leq L. \end{cases} \tag{1.2}$$

Recent studies have significantly advanced the mathematical understanding of the mussel-algae system (1.2) through diverse analytical approaches. Qu et al. [35] established critical thresholds for mussel population persistence versus extinction, identifying explicit dependencies on three key parameters: (i) the energy conversion efficiency γ from algae to mussels, (ii) the advection rate q representing flow velocity, and (iii) the diffusion coefficients d_1 and d_2 governing population dispersal. Their work further characterized the asymptotic stability of positive steady states when they exist. Wang et al. [22] extended this framework by incorporating Danckwerts boundary conditions, with no-flux upstream (at $x = 0$) and free-flow downstream (at $x = L$) for algae, while accounting for intraspecific competition among mussels and analyzing both local and global dynamics. For the non-advective case ($q = 0$), Song et al. [34] conducted a detailed bifurcation analysis, revealing Hopf bifurcations (temporal oscillations), steady-state bifurcations (spatial patterns), and Turing–Hopf bifurcations (spatiotemporal patterns) near constant steady states. In parallel, Shen et al. [36] introduced maturation delays into the diffusive mussel-algae system (1.2), examining the influence of growth response lags on system dynamics. They further established rigorous stability criteria for positive constant steady-state solutions of the delayed mussel-algae system, identifying critical thresholds for delay-induced Hopf bifurcations that generate persistent population oscillations when the digestion period τ exceeds stability boundaries. Subsequently, Shen et al. [37] characterized the emergence of rich spatiotemporal dynamics near Turing–Hopf bifurcation points.

Boundary conditions play a fundamental role in shaping ecological dynamics by controlling population interactions with the environment. In competitive systems, Lou and Lutscher [10] demonstrated that intermediate diffusion rates optimize species persistence in open environments, whereas Lam et al. [9] found that closed environments favor downstream concentration and may benefit from increased diffusion. For predator–prey systems, Nie [19] showed that predator invasion in open advective environments is constrained by a critical flow threshold, while Wang and Nie [38] established that closed systems allow invasion at any advection rate. Nonlinear boundary effects introduce additional complexity. Guo [28,29] revealed that (i) nonlocal delays coupled with boundary conditions can generate Hopf bifurcations when interior reactions dominate, and (ii) stronger boundary outflow accelerates species extinction. These findings have been corroborated in advective environments by Li et al. [39] and Tian et al. [40]. Nevertheless, significant gaps remain in understanding (i) the global dynamics of predator–prey systems with nonlinear boundaries under flow, and (ii) the intricate interplay between advection and boundary fluxes in shaping persistence thresholds and spatial patterns.

The presence of nonlinear boundary conditions in system (1.1) introduces substantial mathematical challenges: (i) standard maximum principle techniques for parabolic systems are no longer directly applicable, and (ii) ill-posedness issues arise that necessitate careful analytical treatment. To overcome these challenges, we adopt a two-pronged approach: by employing techniques compatible with the maximum principle under the structural assumption (H1) governing the nonlinear boundary flux (Theorem 2.1), and developing specialized auxiliary techniques to establish well-posedness (Proposition 3.1). Moreover, nonlinear boundary conditions fundamentally alter the structure of steady states: system (1.1) admits neither trivial nor constant equilibria, precluding the use of standard linear eigenvalue analysis. Instead, we construct super- and sub-solutions to prove the existence of non-constant semi-trivial solutions and analyze their spatial profiles and stability properties. These methods provide a framework for addressing the nontrivial coupling between boundary fluxes and internal reaction–advection–diffusion dynamics.

The goal of this paper is to investigate how the interplay between nonlinear boundary conditions and advection shapes consumer-resource dynamics in system (1.1). Our analysis of the single algae species subsystem (3.1) yields several key insights into boundary-mediated population persistence. Specifically, Proposition 3.1 shows that positive steady states decrease monotonically with increasing flow velocity when advection dominates boundary reactions (i.e., $q > |g(u)|$), contrasting with constant-flux systems [22,35], where monotonicity holds unconditionally. The existence of advection-dependent steady states reveals a critical tradeoff: populations can compensate for strong flow (q) either by increasing dispersal (d_2) or by reducing downstream losses through $g(u)$. In addition, Proposition 3.2 shows that steady-state densities increase with boundary reaction strength, suggesting that boundary flux control strategies (e.g., reducing outflow at $x = L$) can enhance population persistence.

We establish rigorous threshold conditions governing mussel population persistence in system (1.1), characterized by three key parameters: the energy conversion efficiency γ, the advection rate q, and the boundary loss function g. Our analysis reveals that the interplay among these parameters creates distinct dynamical regimes, leading to transitions between extinction and coexistence states. Specifically, we summarize the main findings as follows:

(a) When advection dominates ($q > |g(u)|$), systems with low energy conversion efficiency exhibit mussel extinction across all flow velocities, resulting in algae-only equilibria. In contrast, sufficiently high energy conversion efficiency enables mussel invasion and coexistence under slow flows, while fast flows still lead to extinction (Theorem 4.1). Notably, the special case $g(u) \equiv -q$ recovers previous results [22], demonstrating that our model extends classical homogeneous boundary condition results to more biologically realistic nonlinear settings.

(b) System (1.1) exhibits rich dynamical behaviors arising from the nonlinear coupling among boundary flux g, advection q, energy conversion efficiency γ, and mussel dispersal d_2. In particular, for low γ, a critical mussel diffusion rate d_2^* separates invasion success ($d_2 < d_2^*$) from extinction ($d_2 > d_2^*$), independent of boundary conditions. For high γ, coexistence is promoted when boundary effects dominate advection (i.e., $|g(u)| > q$). Theorem 4.2 demonstrates that mussel persistence is enhanced by both strong boundary retention of algae (large $|g|$) and limited mussel dispersal (small d_2), highlighting the role of spatial confinement in predator establishment under flow.

These results provide new insights into the nonlinear interplay between advective transport and boundary-mediated mechanisms in reaction–diffusion–advection systems with nonlinear boundaries. Our analysis quantitatively characterizes how the balance between downstream drift (controlled by q) and boundary population loss (determined by $g(u)$) shapes ecological outcomes.

The remainder of the paper is organized as follows. In Section 2, we establish global existence and uniform boundedness of solutions to system (1.1). Section 3 focuses on the existence, uniqueness, and global asymptotic stability of semi-trivial steady states. In Section 4, we analyze the effects of energy conversion rate γ, advection rate q, and boundary reaction strength g on global dynamics. Using global bifurcation theory, the existence of coexistence steady states is established in Section 5. Finally, Section 6 summarizes the main results and discusses directions for future research.

2. Global existence and boundedness of solutions

In this section, we establish the global existence and uniform boundedness of solutions to system (1.1) using the super-subsolution method. Our main result is presented in the following theorem.

Theorem 2.1. *Under assumption* (H1), *the following statements hold.*

(i) *For non-negative initial data $\varphi_1(x)$, $\varphi_2(x) \in C([0,L])$, system* (1.1) *admits a unique global solution $(u(x,t), v(x,t))$ defined for all $(x,t) \in [0,L] \times \mathbb{R}_+$. Moreover, if $\varphi_1(x) \not\equiv 0$, $\varphi_2(x) \not\equiv 0$, then $u(x,t) > 0$, $v(x,t) > 0$ for all $(x,t) \in [0,L] \times \mathbb{R}_+$.*

(ii) *The solution remains uniformly bounded, with explicit constants K_1, K_2 (dependent on initial data $\varphi_1(x)$, $\varphi_2(x)$) such that $0 < u(x,t) \le K_1$, $0 < v(x,t) \le K_2$ for $x \in [0,L]$ and $t > 0$.*

Proof. Through the transformation $\beta = \frac{q}{d_1}$ and $\tilde{u}(x,t) = u(x,t)e^{-\beta x}$, system (1.1) can be rewritten as:

$$\begin{cases} \tilde{u}_t = d_1\tilde{u}_{xx} + q\tilde{u}_x + a(e^{-\beta x} - \tilde{u}) - \tilde{u}v, & 0 < x < L, t > 0, \\ v_t = d_2 v_{xx} + \gamma e^{\beta x}\tilde{u}v - \dfrac{v}{1+v}, & 0 < x < L, t > 0, \\ d_1\tilde{u}_x(0,t) = 0, \quad d_1\tilde{u}_x(L,t) = \tilde{u}(L,t)g(e^{\beta L}\tilde{u}(L,t)), & t > 0, \\ v_x(0,t) = v_x(L,t) = 0, & t > 0, \\ \tilde{u}(x,0) = \tilde{u}_0(x) = \varphi_1(x)e^{-\beta x} \ge 0, & \\ \quad \not\equiv 0,\ v(x,0) = \varphi_2(x) \ge 0, \not\equiv 0 & 0 \le x \le L. \end{cases} \tag{2.1}$$

Applying the strong maximum principle and Lemma 2.4 in [29], we establish strict positivity. Namely, for initial data $\varphi_1(x) \ge 0, \not\equiv 0$ and $\varphi_2(x) \ge 0, \not\equiv 0$, the solution $(\tilde{u}(x,t), v(x,t))$ of (2.1) satisfies $\tilde{u}(x,t) > 0$, $v(x,t) > 0$ for $(x,t) \in [0,L] \times \mathbb{R}_+$. Consequently, the original solution $u(x,t) = \tilde{u}(x,t)e^{\beta x}$ maintains positivity throughout the domain.

Next, we show that the solution $(u(x,t), v(x,t))$ is uniformly bounded in $L^\infty((0,L))$. Define

$$P(\tilde{u}, v) = a(e^{-\beta x} - \tilde{u}) - \tilde{u}v, \quad Q(\tilde{u}, v) = \gamma e^{\beta x}\tilde{u}v - \frac{v}{1+v},$$

then $\frac{\partial P}{\partial v} = -\tilde{u} \le 0$, $\frac{\partial Q}{\partial \tilde{u}} = \gamma e^{\beta x} v \ge 0$. Hence, system (2.1) is a mixed quasi-monotone system. We construct a pair of sub- and super-solutions for system (2.1). Let $(\underline{\tilde{u}}(x,t), \underline{v}(x,t)) = (0,0)$ and $(\bar{\tilde{u}}(x,t), \bar{v}(x,t)) = (\bar{\tilde{u}}(t), \bar{v}(t))$ be the unique solution of

$$\begin{cases} \dfrac{\mathrm{d}\tilde{u}}{\mathrm{d}t} = a(1 - \tilde{u}), \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = \gamma e^{\beta L}\tilde{u}v - \dfrac{v}{1+v}, \\ \tilde{u}(0) = \tilde{u}^* = \max\limits_{x\in[0,L]} \tilde{u}_0(x), \quad v(0) = v^* = \max\limits_{x\in[0,L]} \varphi_2(x), \end{cases} \tag{2.2}$$

then by applying Definition 9.7.1 of sub- and super-solutions in [41], we find that $(\underline{\tilde{u}}(x,t), \underline{v}(x,t)) = (0,0)$ and $(\bar{\tilde{u}}(x,t), \bar{v}(x,t)) = (\bar{\tilde{u}}(t), \bar{v}(t))$ are the sub- and super-solution for (2.1), respectively. Then by Theorem 9.7.1 in [41], there exists a unique global solution $(\tilde{u}(x,t), v(x,t))$ of (2.1), which satisfies $0 \le \tilde{u}(x,t) \le \bar{\tilde{u}}(t)$ and $0 \le v(x,t) \le \bar{v}(t)$ for $t > 0$. Thus, we have

$$0 \le u \le \bar{\tilde{u}}(t)e^{\beta x}, \quad 0 \le v \le \bar{v}(t)$$

for $t > 0$.

From [36], for the solution $(\bar{\tilde{u}}(t), \bar{v}(t))$ satisfying system (2.2) and any $\varepsilon > 0$, there exists some $t_0 > 0$ such that $0 < \bar{\tilde{u}}(t) \le 1 + \varepsilon$ for $t > t_0$ and $0 < \bar{v}(t) \le 1 + \varepsilon$ for $t > t_0$. Thus, there exist two positive constants $K_1 := \max\{\max_{x\in[0,L]} \varphi_1(x), e^{\beta L}\}$ and $K_2 := \max\{\max_{x\in[0,L]} \varphi_2(x), 1\}$ such that $0 < \limsup_{t\to+\infty} u(x,t) \le K_1$, $0 < \limsup_{t\to+\infty} v(x,t) \le K_2$ for $x \in [0,L]$. □

3. Semi-trivial steady-state solutions

In this section, we aim to investigate the existence, uniqueness, and stability of semi-trivial steady-state solutions of system (1.1). Our analysis utilizes the super-subsolution method to tackle the mathematical challenges arising from the nonlinear boundary conditions. A key structural feature of system (1.1) is that it admits only two types of steady states: semi-trivial solutions $(u(x), 0)$ and coexistence states $(u(x), v(x))$. Notably, unlike classical cases, system (1.1) possesses neither trivial $(0, 0)$ nor constant steady states, due to the effects of the nonlinear boundary conditions.

3.1. Existence of semi-trivial steady state

We first investigate the existence and uniqueness of semi-trivial steady-state solutions $(u(x), 0)$ of system (1.1). In the mussel-free case (i.e., $v \equiv 0$), the algal population dynamics reduce to a scalar reaction–diffusion–advection system:

$$\begin{cases} u_t = d_1 u_{xx} - q u_x + a(1-u), & 0 < x < L,\ t > 0, \\ d_1 u_x(0,t) - q u(0,t) = 0, & t > 0, \\ d_1 u_x(L,t) - q u(L,t) = u(L,t) g(u(L,t)), & t > 0, \\ u(x,0) = \varphi_1(x) \ge 0,\ \not\equiv 0, & 0 \le x \le L. \end{cases} \tag{3.1}$$

The corresponding steady-state problem is the following elliptic boundary value problem:

$$\begin{cases} d_1 u_{xx} - q u_x + a(1-u) = 0, & 0 < x < L, \\ d_1 u_x(0) - q u(0) = 0, \\ d_1 u_x(L) - q u(L) = u(L) g(u(L)). \end{cases} \tag{3.2}$$

To establish the existence of positive solutions, we introduce the following structural assumption:

(H2) $g(u)$ is strictly decreasing for $u \in (0, \infty)$.

Our first main result demonstrates the existence and uniqueness of algal steady states:

Theorem 3.1. *Under the conditions* (H1) *and* (H2)*, for each* $q \in [0, +\infty)$*,* (3.1) *has a unique positive steady-state solution, denoted by* $u^*(d_1, q, g)(x)$*.*

Proof. Let $\beta = \frac{q}{d_1}$ and $u(x) = e^{\beta x}\tilde{u}(x)$, then system (3.2) can be rewritten as:

$$\begin{cases} d_1 \tilde{u}_{xx} + q\tilde{u}_x + a(e^{-\beta x} - \tilde{u}) = 0, \quad 0 < x < L, \\ d_1 \tilde{u}_x(0) = 0, \quad d_1 \tilde{u}_x(L) = \tilde{u}(L) g(e^{\beta L}\tilde{u}(L)). \end{cases} \tag{3.3}$$

Set $\underline{\tilde{u}}(x) = 0 < 1$ and $\overline{\tilde{u}}(x) = 1$, then $\underline{\tilde{u}}(x)$ satisfies

$$\begin{cases} -d_1 \underline{\tilde{u}}_{xx} - q\underline{\tilde{u}}_x - a(e^{-\beta x} - \underline{\tilde{u}}) = -ae^{-\beta x} < 0, \quad 0 < x < L, \\ -d_1 \underline{\tilde{u}}_x(0) = 0 \le 0, \quad d_1 \underline{\tilde{u}}_x(L) - \underline{\tilde{u}}(L) g(e^{\beta L}\underline{\tilde{u}}(L)) = 0 \le 0, \end{cases}$$

and $\overline{\tilde{u}}(x)$ satisfies

$$\begin{cases} -d_1 \overline{\tilde{u}}_{xx} - q\overline{\tilde{u}}_x - a(e^{-\beta x} - \overline{\tilde{u}}) = -a(e^{-\beta x} - 1) > 0, \quad 0 < x < L, \\ -d_1 \overline{\tilde{u}}_x(0) = 0 \ge 0, \quad d_1 \overline{\tilde{u}}_x(L) - \overline{\tilde{u}}(L) g(e^{\beta L}\overline{\tilde{u}}(L)) = -g(e^{\beta L}\overline{\tilde{u}}(L)) \ge 0. \end{cases}$$

By applying Definition 4.4.1 of sub- and super-solutions from [41], we observe that the constant functions $\underline{\tilde{u}}(x) = 0$ and $\overline{\tilde{u}}(x) = 1$ serve as sub- and super-solutions, respectively, for problem (3.3). Through the comparison principle for elliptic equations with nonlinear boundary conditions (Theorem 4.4.1 in [41]), we conclude that (3.3) admits at least one positive solution $\tilde{u}^*(d_1, q, g)(x)$ satisfying $0 < \tilde{u}^*(d_1, q, g)(x) < 1$ for all $q \in [0, +\infty)$. Consequently, the original Eq. (3.2) possesses a corresponding positive solution $u^*(d_1, q, g)(x)$ bounded by $0 < u^*(d_1, q, g)(x) < e^{\beta x}$.

To establish the uniqueness of positive solutions to (3.2), we proceed by contradiction. Suppose there exist two distinct positive solutions, denoted by $\tilde{u}_1^*(x)$ and $\tilde{u}_2^*(x)$, with $\tilde{u}_1^*(x) \neq \tilde{u}_2^*(x)$. Without loss of generality, we assume $\tilde{u}_1^*(x) < \tilde{u}_2^*(x)$ on some $(0, L)$. Since $\tilde{u}_1^*(x)$ is a steady-state solution of (3.2), it is a positive solution to

$$\begin{cases} d_1 \phi_{xx} - q\phi_x + a(1 - \tilde{u}_1^*) = \mu\phi, \quad 0 < x < L, \\ d_1 \phi_x(0) - q\phi(0) = 0, \\ d_1 \phi_x(L) - q\phi(L) = \phi(L) g(\tilde{u}_1^*(L)). \end{cases} \tag{3.4}$$

with $\mu = 0$, so that $\mu_1 = 0$ is the first eigenvalue for (3.4). Similarly, $\tilde{u}_2^*(x)$ satisfies

$$\begin{cases} d_1 \phi_{xx} - q\phi_x + a(1 - \tilde{u}_2^*) = \mu\phi, \quad 0 < x < L, \\ d_1 \phi_x(0) - q\phi(0) = 0, \\ d_1 \phi_x(L) - q\phi(L) = \phi(L) g(\tilde{u}_2^*(L)). \end{cases} \tag{3.5}$$

with $\mu = 0$, so that $\mu_1 = 0$ is the first eigenvalue for (3.5). However, since $a(1 - \tilde{u}_1^*) > a(1 - \tilde{u}_2^*)$ and $g(u)$ is strictly decreasing in u and $\tilde{u}_1^*(x) < \tilde{u}_2^*(x)$ on at least part of $(0, L)$, the first eigenvalue of (3.5) must be strictly less than that of (3.4), contradicting the fact that both systems have $\mu_1 = 0$ as their principal eigenvalue. Therefore, our initial assumption is false, and we conclude that $\tilde{u}_1^*(x) \equiv \tilde{u}_2^*(x)$. Therefore, (3.1) has a unique positive steady-state solution $u^*(d_1, q, g)(x)$. ☐

The global existence and uniqueness of solutions of (1.1) follow directly from Theorem 2.1. That is to say, for any initial data $\varphi = (\varphi_1, \varphi_2) \in C([0, L], \mathbb{R}_2)$, there exists a unique solution $u^\varphi = (u^\varphi(x,t), v^\varphi(x,t))$ of (1.1), defined on $[0, L] \times \mathbb{R}_+$, and satisfying $u^\varphi(\cdot, t) \in C([0, L], \mathbb{R}_2)$ for all $t \in \mathbb{R}_+$. This allows us to define an associated solution semigroup $\{T_t : t \ge 0\}$ in $C([0, L], \mathbb{R}_2)$ by $T_t\varphi = u^\varphi(\cdot, t)$ for $t \ge 0$.

Regarding the asymptotic behavior, Theorem 3.1 implies that system (3.1) admits a unique positive steady state $u^*(d_1, q, g)(x)$. The long-term dynamics of solutions $u(x,t)$ are governed by the semi-flow generated by (3.1). As (3.1) constitutes a gradient system, we may apply fundamental results from dynamical systems theory [42] combined with Lemma 2.2.1 in [43] to immediately obtain the following global stability result:

Theorem 3.2. *Under assumptions* (H1) *and* (H2)*, the steady state* $u^*(d_1, q, g)(x)$ *is globally asymptotically stable for system* (3.1)*.*

3.2. Properties of the positive steady state

We now examine the qualitative properties of the positive steady-state solution $u^*(d_1, q, g)(x)$ of (3.1). The following proposition establishes several key analytical results:

Proposition 3.1. *Under assumptions* (H1) *and* (H2)*, the following three statements are true:*

(i) *Boundedness:* $0 < u^*(d_1, q, g)(x) < e^{\beta x}$ *for all* $x \in (0, L)$*.*

(ii) *Gradient bounds: If* $g(u) \ge -q$ *for all* $u \in \mathbb{R}$*, then* $0 < u_x^*(d_1, q, g)(x) < \beta u^*(d_1, q, g)(x)$ *in* $(0, L)$*.*

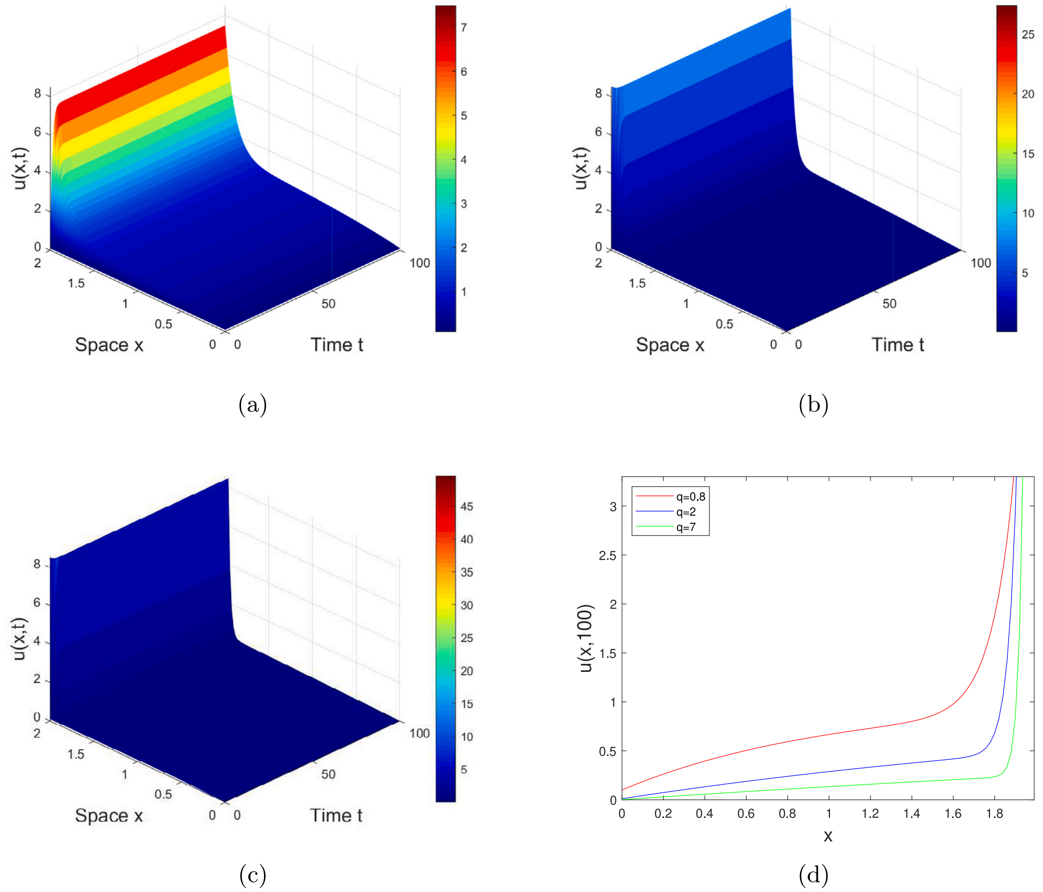
(iii) *Advection dependence: If* $g(u) \ge -q$ *for all* $u \in \mathbb{R}$*, then* $u^*(d_1, q, g)(x)$ *is decreasing in* q *on* $[0, L]$*. Furthermore, for* $1 < \gamma < 1/a$*, there exist positive constants* C_2 *and* C_3 *independent of* q *such that*

$$\exp\left\{-\left(\frac{C_3}{q} + \frac{q}{d_1}\right)(L - x)\right\} \le \frac{u^*(d_1, q, g)(x)}{u^*(d_1, q, g)(L)} \le \exp\left\{\left(\frac{C_2}{q} - \frac{q}{d_1}\right)(L - x)\right\} \tag{3.6}$$

for all $x \in [0, L]$*. Moreover, we have the asymptotic behavior:*

$$\lim_{q \to \infty} \left\| u^*(d_1, q, g)(x) - u^*(d_1, q, g)(L) \exp\left\{-\frac{q}{d_1}(L - x)\right\} \right\|_{L^\infty((0,L))} = 0, \tag{3.7}$$

indicating uniform convergence to zero on compact subsets of $[0, L)$ *as* $q \to \infty$*.*



(a)

(b)

(c)

(d)

Fig. 1. The positive steady-state solution of (3.1) with $L = 2$, $d_1 = 0.1$, $a = 1$, $g(u) = e^{-u} - 0.1$, $\varphi_1 = 0.1$ and different values of q: (a) $q = 0.8$, (b) $q = 2$, (c) $q = 7$. (d) the spatial profile corresponding to (a)–(c) for fixed time $t = 100$.

Proof. The boundedness follows directly from Theorem 3.1. For part (ii), set $w := \frac{u_x^*}{u^*}$, then w satisfies

$$\begin{cases} -d_1 w_{xx} + (q - 2d_1 w)w_x + aw\dfrac{1}{u^*} = 0, & 0 < x < L, \\ w(0) = \dfrac{q}{d_1} > 0, \quad w(L) = \dfrac{q + g(u^*)}{d_1} \geq 0, \end{cases} \tag{3.8}$$

where $g(u) \geq -q$ for all $u \in \mathbb{R}$. The maximum principle yields $0 < w := \frac{u_x^*}{u^*} < \frac{q}{d_1}$ on $(0, L)$, that is, $0 < u_x^*(d_1, q, g)(x) < \beta u^*(d_1, q, g)(x)$ in $(0, L)$. From (3.3) and part (ii), we have $(\tilde{u}^*)_x = e^{-\beta x}(-\beta u^* + u_x^*) < 0$ when $g(u) \geq -q$ for all $u \in \mathbb{R}$. For part (iii), differentiating (3.3) with respect to q, denoting $\frac{\partial}{\partial q} ='$, we obtain

$$\begin{cases} -d_1(\tilde{u}^*)'_{xx} - q(\tilde{u}^*)'_x + \dfrac{a}{d_1}e^{\beta x}x + a(\tilde{u}^*)' = (\tilde{u}^*)_x, & 0 < x < L, \\ -d_1(\tilde{u}^*)'_x(0) = 0, \\ d_1(\tilde{u}^*)'_x(L) - (\tilde{u}^*)'(L)[g(e^{\beta L}\tilde{u}^*(L)) + e^{\beta L}\tilde{u}^*(L)g'(e^{\beta L}\tilde{u}^*(L))] \\ \quad = \dfrac{L}{d_1}e^{\beta L}g'(e^{\beta L}\tilde{u}^*(L))(\tilde{u}^*)^2(L), \end{cases} \tag{3.9}$$

where $g(u) \geq -q$ for all $u \in \mathbb{R}$. Let $\theta = (\tilde{u}^*)'$, then (3.9) can be transformed as follows

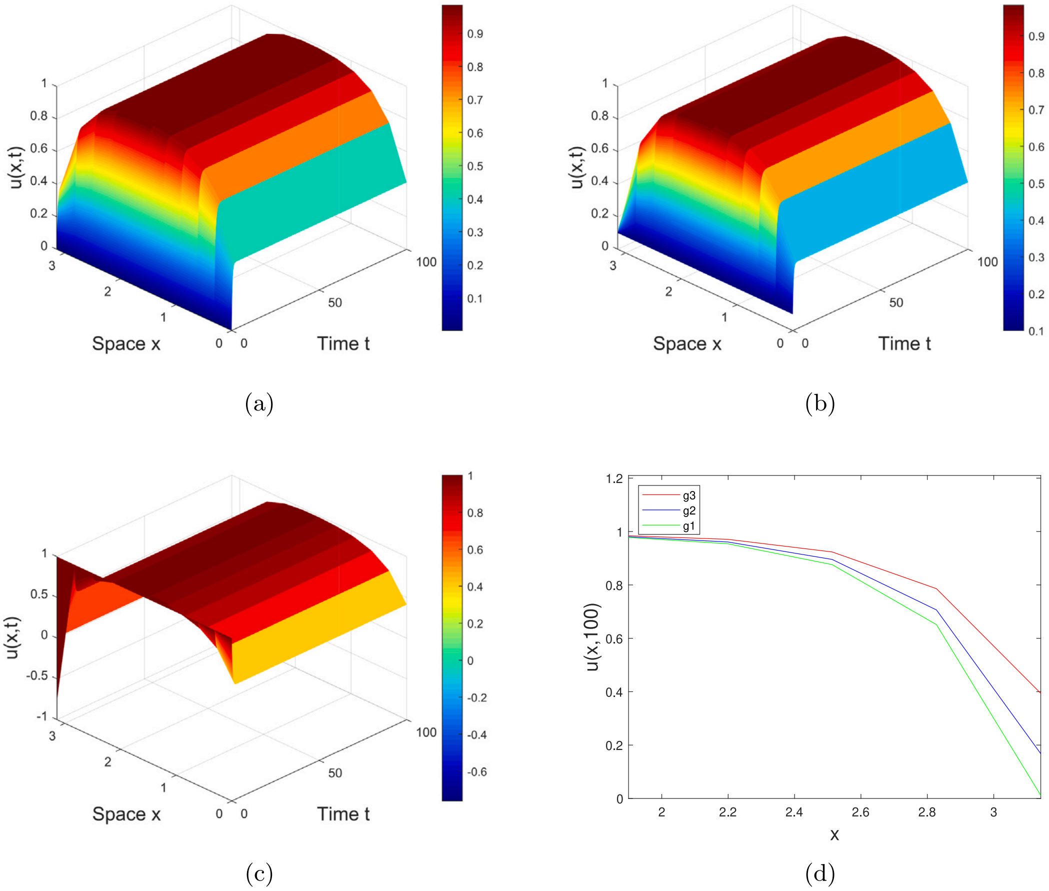
$$\begin{cases} -d_1\theta_{xx} - q\theta_x + a\theta + \dfrac{a}{d_1}e^{\beta x}x = (\tilde{u}^*)_x, & 0 < x < L, \\ -d_1\theta_x(0) = 0, \\ d_1\theta_x(L) - \theta(L)[g(e^{\beta L}\tilde{u}^*(L)) + e^{\beta L}\tilde{u}^*(L)g'(e^{\beta L}\tilde{u}^*(L))] \\ \quad = \dfrac{L}{d_1}e^{\beta L}g'(e^{\beta L}\tilde{u}^*(L))(\tilde{u}^*)^2(L), \end{cases} \tag{3.10}$$

By similar arguments as Theorem 3.1, system (3.10) has a super-solution $\overline{\theta}(x) = 0$ and sub-solution $\underline{\theta}(x) = -M$, where $M > 0$ is sufficiently large. The comparison principle of elliptic equations (see, e.g. [41]) implies that system (3.10) has at least a solution $\theta(x)$, which satisfies $-M < \theta(x) < 0$. Then by the strong maximum principle, we have $\theta(x) < 0$. Namely, $(\tilde{u}^*)'(x) < 0$ on $[0, L]$, i.e., $(u^*)'(x) < 0$ on $[0, L]$. Thus, $u^*(d_1, q, g)(x)$ is decreasing with respect to q pointwisely on $[0, L]$. From the Lemma 5.6 and Theorem 5.7 in [35], if $1 < \gamma < 1/a$, we can obtain (3.6) and (3.7). The proof is completed. □

Remark 3.1. From Proposition 3.1, the condition $g(u) \geq -q$ for all $u \geq 0$ implies that the unique positive steady state decreases with respect to the advection rate q only when the downstream flow dominates the algal flux. More complex behavior arises when the algal flux oscillates around the advection values, suggesting rich dynamics that merit further investigation. Numerical simulation results illustrating the monotonicity are shown in Fig. 1.

Proposition 3.2. *Under assumptions* (H1) *and* (H2)*, the positive steady-state solution* $u^*(d_1, q, g)(x)$ *is monotonically increasing with respect to the boundary flux function* g *on* $[0, L]$.

Proof. Let u_1^* and u_2^* be the unique positive steady-state solution of (3.1) corresponding to boundary flux functions g_1 and g_2, respectively,



(a) (b) (c) (d)

Fig. 2. The positive steady-state solution of (3.1) with $L = \pi$, $d_1 = 0.1$, $a = 1$, $q = 0.1$, $\varphi_1 = 0.1$ and different values of $g(u)$. (a) $g_1(u) = -6u - 10$, (b) $g_2(u) = -u - 3$, (c) $g_3(u) = -0.1u - 1$. (d) the spatial profile corresponding to (a)–(c) for fixed time $t = 100$.

that is, u_2^* satisfies the following equations:

$$\begin{cases} d_1 u_{2xx}^* - q u_{2x}^* + a(1 - u_2^*) = 0, \quad 0 < x < L, \\ d_1 u_{2x}^*(0) - q u_2^*(0) = 0, \\ d_1 u_{2x}^*(L) - q u_2^*(L) = u_2^*(L) g_2(u_2^*(L)). \end{cases} \tag{3.11}$$

Suppose that $g_1(u) < g_2(u)$ for all $u > 0$. From the boundary conditions at $x = L$, we have

$$\begin{aligned} 0 &= d_1 u_{1x}^*(L) - q u_1^*(L) - u_1^* g_1(u_1^*(L)) \\ &> d_1 u_{1x}^*(L) - q u_1^*(L) - u_1^* g_2(u_1^*(L)), \end{aligned} \tag{3.12}$$

then

$$\begin{cases} d_1 u_{1xx}^* - q u_{1x}^* + a(1 - u_1^*) = 0, \quad 0 < x < L, \\ d_1 u_{1x}^*(0) - q u_1^*(0) = 0, \\ d_1 u_{1x}^*(L) - q u_1^*(L) - u_1^*(L) g_2(u_1^*(L)) < 0. \end{cases} \tag{3.13}$$

This shows that u_1^* serves as a strict subsolution for (3.11). Since system (3.11) admits a unique equilibrium u^{**} with $u^{**} > u_1^*$. Since u_2^* is the unique positive equilibrium for (3.11), we conclude $u_2^* = u^{**} > u_1^*$ pointwise on $[0, L]$. Therefore, $u^*(d_1, q, g)(x)$ is monotonically increasing with respect to g pointwisely on $[0, L]$. ☐

Remark 3.2. Proposition 3.2 demonstrates that algal persistence is enhanced by reducing downstream boundary loss (i.e., by increasing g). This suggests that management strategies aimed at minimizing outflow at $x = L$ could promote the stability of the algal population. Numerical simulations presented in Fig. 2 support these theoretical findings.

3.3. Stability of semi-trivial steady-states

The purpose of this subsection is to investigate the stability properties of the semi-trivial steady-state solution $(u^*(d_1, q, g), 0)$ of system (1.1), as established in Theorem 3.1. The linear stability is determined by analyzing the associated eigenvalue problem:

$$\begin{cases} d_1 \phi_{xx} - q\phi_x - a\phi - u^*(d_1, q, g)\psi = \lambda\phi, \quad 0 < x < L, \\ d_2 \psi_{xx} + [\gamma u^*(d_1, q, g) - 1]\psi = \lambda\psi, \quad 0 < x < L, \\ d_1 \phi_x(0) - q\phi(0) = 0, \\ d_1 \phi_x(L) - q\phi(L) = \phi(L)[g(u^*(d_1, q, g)(L)) \\ \quad + u^*(d_1, q, g)(L) g'(u^*(d_1, q, g)(L))], \\ \psi_x(0) = \psi_x(L) = 0. \end{cases} \tag{3.14}$$

Note that the second equation is decoupled from the first. By Lemma 3.2 of [19], it is straightforward to see that the eigenvalues of (3.14) consist of those arising from the following two separate eigenvalue problems:

$$\begin{cases} d_1 \phi_{xx} - q\phi_x - a\phi = \lambda\phi, \quad 0 < x < L, \\ d_1 \phi_x(0) - q\phi(0) = 0, \\ d_1 \phi_x(L) - q\phi(L) = \phi(L)[g(u^*(d_1, q, g)(L)) \\ \quad + u^*(d_1, q, g)(L) g'(u^*(d_1, q, g)(L))], \end{cases} \tag{3.15}$$

and

$$\begin{cases} d_2 \psi_{xx} + [\gamma u^*(d_1, q, g) - 1]\psi = \lambda\psi, \quad 0 < x < L, \\ \psi_x(0) = \psi_x(L) = 0. \end{cases} \tag{3.16}$$

Under assumptions (H1) and (H2), integration (3.15) over $(0,L)$ yields

$$\lambda_1^{\phi}\int_0^L \phi \mathrm{d}x = [g(u^*(d_1,q,g)(L)) + u^*(d_1,q,g)(L)g'(u^*(d_1,q,g)(L))] \times \phi(L) - a\int_0^L \phi \mathrm{d}x < 0, \tag{3.17}$$

which implies that the principal eigenvalue λ_1^{ϕ} of (3.15) is negative. Thus, the stability of $(u^*(d_1,q,g),0)$ depends entirely on the principal eigenvalue $\lambda_1(d_1,d_2,q,g,\gamma)$ of (3.16), characterized variationally as (see, e.g., [23]):

$$\lambda_1(d_1,d_2,q,g,\gamma) = \sup_{0\neq\psi\in W^{1,2}(0,L)} \frac{\int_0^L [\gamma u^*(d_1,q,g)-1]\psi^2\mathrm{d}x - d_2\int_0^L(\psi_x)^2\mathrm{d}x}{\int_0^L \psi^2\mathrm{d}x}. \tag{3.18}$$

Consequently, we have

Proposition 3.3. *Under assumptions* (H1) *and* (H2)*, let* $\lambda_1(d_1,d_2,q,g,\gamma)$ *be the principal eigenvalue of* (3.16)*. Then the semi-trivial steady state* $(u^*(d_1,q,g),0)$ *is linearly stable if* $\lambda_1(d_1,d_2,q,g,\gamma)<0$*, is neutrally stable if* $\lambda_1(d_1,d_2,q,g,\gamma)=0$ *and is linearly unstable if* $\lambda_1(d_1,d_2,q,g,\gamma)>0$*.*

Furthermore, due to the special structure of the consumer-resource system (1.1), the comparison principle can be employed to show that the semi-trivial steady state $(u^*(d_1,q,g),0)$ is globally stable whenever it is locally asymptotically stable.

Proposition 3.4. *Under assumptions* (H1) *and* (H2)*, the semi-trivial steady-state* $(u^*(d_1,q,g),0)$ *is globally stable for system* (1.1) *as long as it is locally asymptotically stable.*

Proof. Let $U(x,t)$ be the solution of

$$\begin{cases} U_t = d_1U_{xx} - qU_x + a(1-U), & 0<x<L, t>0,\\ d_1U_x(0,t) - qU(0,t) = 0, & t>0,\\ d_1U_x(L,t) - qU(L,t) = U(L,t)g(U(L,t)), & t>0,\\ U(x,0) = \varphi(x) \geq 0, \not\equiv 0, & 0\leq x\leq L, \end{cases} \tag{3.19}$$

and $u(x,t)$ satisfies system (1.1), then

$$\begin{aligned} &U_t - d_1U_{xx} + qU_x - a(1-U) = 0 \geq -uv = u_t - d_1u_{xx} + qu_x - \alpha(1-u),\\ &\quad 0<x<L, t>0,\\ &d_1U_x(0,t) - qU(0,t) = 0 = d_1u_x(0,t) - qu(0,t), \quad t>0,\\ &d_1U_x(L,t) - qU(L,t) - U(L,t)g(U(L,t)) = 0 = d_1u_x(L,t)\\ &\quad - qu(L,t) - u(L,t)g(u(L,t)), \quad t>0,\\ &U(x,0) = \varphi(x) = u(x,0), \quad 0\leq x\leq L. \end{aligned}$$

By the comparison principle of parabolic systems [41], we have $u(x,t)\leq U(x,t)$ for $t>0$. By Theorem 3.2, we have

$$\lim_{t\to+\infty} U(x,t) = u^*(d_1,q,g)(x).$$

Denote $u^*(d_1,q,g)$ by u^* and let $\lambda_1^{u^*}$ be the principal eigenvalue of the linearized eigenvalue problem (3.14). Since $u^*(d_1,q,g)$ is locally asymptotically stable, we have $\lambda_1^{u^*}<0$. Choose $\epsilon_0>0$, such that $\lambda_1^{u^*+\epsilon_0}<0$, where $\epsilon_0=\epsilon_1+\epsilon_2$, $0<\epsilon_1\ll 1$ and $0<\epsilon_2\ll 1$. Then there exists $T>0$ such that

$$u(x,t)\leq u^*(x)+\epsilon_1 \quad \text{and} \quad \frac{1}{1+v(x,t)} \geq 1-\gamma\epsilon_2$$

for $t\geq T$. By the second equation in (1.1), we have

$$v_t \leq d_2v_{xx} + \gamma(u^*+\epsilon_1)v - v(1-\gamma\epsilon_2), \quad 0<x<L, t\geq T,$$

then

$$\begin{cases} v_t \leq d_2v_{xx} + [\gamma(u^*+\epsilon_0)-1]v, & 0<x<L, t\geq T,\\ v_x(0,T) = v_x(L,T) = 0,\\ v(x,T) \leq C\phi_{1v}(x), & 0<x<L, \end{cases} \tag{3.20}$$

where $C>0$ is large enough and $\phi_{1v}(x)$ is a positive principal eigenfunction associated with the principal eigenvalue $\lambda_1^{u^*+\epsilon_0}(d_1,d_2,q,g,\gamma)$ in (3.16). Let $V(x,t)$ be the solution of the problem

$$\begin{cases} V_t = d_2V_{xx} + [\gamma(u^*+\epsilon_0)-1]V, & 0<x<L, t\geq T,\\ V_x(0,T) = V_x(L,T) = 0,\\ V(x,T) = C\phi_{1v}(x), & 0<x<L, \end{cases} \tag{3.21}$$

then by the comparison principle of parabolic systems [41], we have $v(x,t)\leq V(x,t)$. It is easy to check that the solution of (3.21) is

$$V(x,t) = C\phi_{1v}(x)e^{\lambda_1^{u^*+\epsilon_0}(t-T)}.$$

Since $\lambda_1^{u^*+\epsilon_0}<0$, we have $\lim_{t\to+\infty}V(x,t)=0$, which implies $\lim_{t\to+\infty} v(x,t)=0$. By the theory of asymptotically autonomous semi-flows [42], we have $\lim_{t\to+\infty}u(x,t)=u^*(d_1,q,g)(x)$. □

From Propositions 3.3 and 3.4, we can immediately obtain the following threshold dynamics of system (1.1).

Theorem 3.3. *Under assumptions* (H1) *and* (H2)*, the semi-trivial steady-state* $(u^*(d_1,q,g),0)$ *of* (1.1) *is globally asymptotically stable when* $\lambda_1(d_1,d_2,q,g,\gamma)<0$*, and is unstable when* $\lambda_1(d_1,d_2,q,g,\gamma)>0$*.*

4. Classification of dynamical behaviors

In this section, we investigate the parameter dependence of the principal eigenvalue $\lambda_1(d_1,d_2,q,g,\gamma)$ in (3.16), which governs the global dynamics according to Theorem 3.3.

To study the eigenvalue problem (3.16), we consider the following linear eigenvalue problem:

$$\begin{cases} d\omega_{xx} + h(x)\omega = \mu\omega, & 0<x<L,\\ \omega_x(0) = \omega_x(L) = 0, \end{cases} \tag{4.1}$$

where $d>0$ and $h(\cdot)\in C([0,L])$. It is well known (see, e.g., [23]) that problem (4.1) admits a principal eigenvalue, denoted by $\mu_1(d,h)$, which has an associated eigenfunction $\omega_1(d,h)$. The principal eigenpair $(\mu_1(d,h),\omega_1(d,h))$ possesses the following properties:

Lemma 4.1 (*[19]*)**.** *Suppose that* $d>0$ *and* $h(\cdot)\in C([0,L])$*. Let* $\mu_1(d,h)$ *be the principal eigenvalue of eigenvalue problem* (4.1)*, then*

- **(i)** *Smooth dependence:* $\mu_1(d,h)$ *and* $\omega_1(d,h)$ *depend continuously and smoothly on* d*;*
- **(ii)** *Continuity: if* $\| h_n(\cdot)-h(\cdot)\|_\infty \to 0$ *with* $h_n(\cdot)\in L^\infty((0,L))$*, then* $\mu_1(d,h_n)\to\mu_1(d,h)$*;*
- **(iii)** *Monotonicity:* $h_1(x)\geq h_2(x)$ *implies* $\mu_1(d,h_1)\geq\mu_1(d,h_2)$*, and the equality holds only if* $h_1(x)\equiv h_2(x)$*;*
- **(iv)** *Asymptotics:* $\mu_1(d,h)$ *is strictly decreasing with respect to* d *if* $h(x)$ *is not a constant. Moreover,* $\lim_{d\to 0}\mu_1(d,h)=\max_{x\in[0,L]}h(x)$ *and* $\lim_{d\to\infty}\mu_1(d,h)=\frac{1}{L}\int_0^L h(x)\mathrm{d}x$*;*
- **(v)** *Constant case: If* $h(x)\equiv h_0$ *is a constant, then* $\mu_1(d,h)=h_0$*.*

Using similar arguments as for Proposition 3.1 in [23], one can conclude that the principal eigenvalue of (3.16), denoted by $\lambda_1(d_1,d_2,q,g,\gamma)$, depends continuously and smoothly on d_1,d_2,q,g,γ, and its associated eigenfunction, denoted by $\psi_1(d_1,d_2,q,g,\gamma)$, can be chosen to be strictly positive on $[0,L]$. Indeed,

$$\lambda_1(d_1,d_2,q,g,\gamma) = \mu_1(d_2,\gamma u^*(d_1,q,g)-1) \tag{4.2}$$

Furthermore, the principal eigen-pair $(\lambda_1(d_1,d_2,q,g,\gamma),\psi_1(d_1,d_2,q,g,\gamma))$ has the following properties.

Lemma 4.2. *Suppose that assumptions* (H1) *and* (H2) *hold. Let* $\lambda_1(d_1, d_2, q, g, \gamma)$ *be the principal eigenvalue of eigenvalue problem* (3.16)*. Then the following three statements are true.*

- **(i)** *Advection dependence: If* $g(u) \geq -q$ *for all* $u \in \mathbb{R}$, *then* $\lambda_1(d_1, d_2, q, g, \gamma)$ *is strictly decreasing with respect to* q *in* $[0, +\infty)$*. Moreover,* $\lim_{q\to+\infty} \lambda_1(d_1, d_2, q, g, \gamma) = -1$.
- **(ii)** *Boundary flux dependence:* $\lambda_1(d_1, d_2, q, g, \gamma)$ *is non-decreasing with respect to* g *in* $(-\infty, 0]$.
- **(iii)** *Diffusion/growth dependence:* $\lambda_1(d_1, d_2, q, g, \gamma)$ *is strictly decreasing with respect to* d_2 *in* $(0, +\infty)$*, and* $\lambda_1(d_1, d_2, q, g, \gamma)$ *is strictly increasing with respect to* γ *in* $(0, +\infty)$*. Moreover,*

$$\lim_{d_2\to 0} \lambda_1(d_1, d_2, q, g, \gamma) = \gamma \max\nolimits_{x\in[0,L]} u^*(d_1, q, g)(x) - 1$$

and

$$\lim_{d_2\to \infty} \lambda_1(d_1, d_2, q, g, \gamma) = \frac{\gamma}{L}\int_0^L u^*(d_1, q, g)(x)\mathrm{d}x - 1.$$

Proof. (i) In view of (4.2), one can conclude that assertion (i) holds by combining with Proposition 3.1 (iii). For readers convenience, we give the detailed proof here. In fact, by the implicit function theorem, $\psi_1(d_1, d_2, q, g, \gamma)$ is a smooth function of q from $[0, +\infty)$ into $C^2([0, L])$ [44].

For simplicity, denote $u^*(d_1, q, g)$ by u^*, $\lambda_1(d_1, d_2, q, g, \gamma)$ by λ_1, $\psi_1(d_1, d_2, q, g, \gamma)$ by ψ_1, $\frac{\partial}{\partial q}u^*(d_1, q, g)$ by $(u^*)'$, $\frac{\partial}{\partial q}\psi_1(d_1, d_2, q, g, \gamma)$ by ψ_1'. Differentiating (3.16) with respect to q, denoting $\frac{\partial}{\partial q} = '$, we find

$$\begin{cases} d_2(\psi_1')_{xx} + \gamma(u^*)'\psi_1 + (\gamma u^* - 1)\psi_1' = \lambda_1\psi_1' + \lambda_1'\psi_1, & 0 < x < L, \\ (\psi_1')_x(0) = (\psi_1')_x(L) = 0. \end{cases} \tag{4.3}$$

Multiplying (4.3) by ψ_1, (3.16) by ψ_1', integrating over $(0, L)$ and subtracting the two equations, we have

$$\lambda_1' \int_0^L \psi_1^2 \mathrm{d}x = \gamma \int_0^L (u^*)'\psi_1^2 \mathrm{d}x < 0$$

since $\frac{\partial u^*(d_1,q,g)}{\partial q} < 0$ when $g(u) \geq -q$ for all $u \in \mathbb{R}$ (see Proposition 3.1 (iii)). That is, $\lambda_1(d_1, d_2, q, g, \gamma)$ is strictly decreasing with respect to q in $[0, +\infty)$ if $g(u) \geq -q$ for all $u \in \mathbb{R}$. Note that $u^*(x) \to 0$ uniformly in any compact subset of $[0, L)$ as $q \to \infty$ (see Proposition 3.1 (iii)), we can easily get that

$$\lim_{q\to+\infty} \lambda_1(d_1, d_2, q, g, \gamma) = \lim_{q\to+\infty} \mu_1(d_2, \gamma u^*(d_1, q, g) - 1) = \mu_1(d_2, -1) = -1.$$

(ii) By Lemma 4.1 (iii), $\mu_1(d_2, \gamma u^*(d_1, q, g) - 1)$ is non-decreasing to u^*. Since $u^*(d_1, q, g)$ is strictly increasing in g on $[0, L]$ (see Proposition 3.2), then $\mu_1(d_2, \gamma u^*(d_1, q, g) - 1)$ is non-decreasing with respect to g. Thus, by (4.2), $\lambda_1(d_1, d_2, q, g, \gamma)$ is non-decreasing with respect to g in $(-\infty, 0]$.

The first part of conclusion (iii) is a direct result of Lemma 4.1 (iv). Note that

$$\lim_{d\to 0} \mu_1(d, h) = \max_{x\in[0,L]} h(x) \quad \text{and} \quad \lim_{d\to\infty} \mu_1(d, h) = \frac{1}{L}\int_0^L h(x)\mathrm{d}x$$

(see Lemma 4.1 (iv)), then it follows from Lemma 4.1 (v) that

$$\lim_{d_2\to 0} \lambda_1(d_1, d_2, q, g, \gamma) = \lim_{d_2\to 0} \mu_1(d_2, \gamma u^*(d_1, q, g) - 1) = \gamma \max_{x\in[0,L]} u^*(d_1, q, g)(x) - 1$$

and

$$\lim_{d_2\to \infty} \lambda_1(d_1, d_2, q, g, \gamma) = \lim_{d_2\to \infty} \mu_1(d_2, \gamma u^*(d_1, q, g) - 1) = \frac{\gamma}{L}\int_0^L u^*(d_1, q, g)(x)\mathrm{d}x - 1.$$

The proof is completed. □

These results completely characterize the sign of $\lambda_1(d_1, d_2, q, g, \gamma)$ in terms of the key parameters γ, q, d_2, and the function g, which govern the system's global dynamics according to Theorem 3.3. The monotonicity properties reveal how different ecological factors influence population persistence: stronger advection promotes extinction, reduced downstream loss supports persistence, intermediate mussel mobility optimizes survival, and higher energy conversion facilitates coexistence.

4.1. Threshold dynamics governed by energy conversion and advection

Theorem 4.1. *In addition to the condition* (H1)*, suppose that* $g(u) \geq -q$, $g(1) = 0$ *and* $g(u)$ *is strictly decreasing in* $u \in [1, \infty)$*, then the following statements hold:*

- **(i)** *If* $\gamma \leq 1$ *(i.e., low conversion efficiency),* $(u^*(d_1, q, g), 0)$ *is globally asymptotically stable for* $q \in [0, +\infty)$.
- **(ii)** *If* $\gamma > 1$ *(i.e., high conversion efficiency), then there exists* $q_0 \in (0, +\infty)$ *continuously depending on* d_1, d_2, γ*, such that* $(u^*(d_1, q, g), 0)$ *is globally asymptotically stable if* $q \in (q_0, +\infty)$*, and unstable if* $q \in [0, q_0)$.

Proof. Since $g(1) = 0$, we have $\lim_{q\to 0} u^*(d_1, q, g) = 1$ uniformly on $[0, L]$. From Lemma 4.1 (v), we can easily conclude that

$$\lambda_1(d_1, d_2, 0, g, \gamma) = \mu_1(d_2, \gamma u^*(d_1, 0, g) - 1) = \mu_1(d_2, \gamma - 1) = \gamma - 1.$$

If $\gamma \leq 1$, the monotonicity of $\lambda_1(d_1, d_2, q, g, \gamma)$ with respect to q (see Lemma 4.2(i)) implies that for any $q \in [0, +\infty)$,

$$\lambda_1(d_1, d_2, q, g, \gamma) < \lambda_1(d_1, d_2, 0, g, \gamma) = \gamma - 1 \leq 0,$$

which implies $(u^*(d_1, q, g), 0)$ is globally asymptotically stable.

If $\gamma > 1$, we have $\lambda_1(d_1, d_2, 0, g, \gamma) > 0$. Note that $\lim_{q\to+\infty} \lambda_1(d_1, d_2, q, g, \gamma) = -1$. By Lemma 4.2(i) and the implicit function theorem, we can conclude that there exists a unique $q_0 \in (0, +\infty)$ continuously depending on d_1, d_2, γ, such that

$$\begin{cases} \lambda_1(d_1, d_2, q, g, \gamma) > 0, & \text{if } 0 \leq q < q_0, \\ \lambda_1(d_1, d_2, q, g, \gamma) = 0, & \text{if } q = q_0, \\ \lambda_1(d_1, d_2, q, g, \gamma) < 0, & \text{if } q > q_0. \end{cases} \tag{4.4}$$

Namely, for $\gamma > 1$, we have $(u^*(d_1, q, g), 0)$ is globally asymptotically stable if $q \in (q_0, +\infty)$, and it is unstable if $q \in [0, q_0)$. □

Proposition 4.1. *Under the conditions of* Theorem 4.1*, suppose that* $\gamma > 1$*. Then* $q_0(d_1, d_2, \gamma)$*, is uniquely determined by*

$$\lambda_1(d_1, d_2, q_0, g, \gamma) = 0, \tag{4.5}$$

and is strictly increasing with respect to γ *in* $(1, +\infty)$ *with* $q_0(d_1, d_2, 1) = 0$.

Proof. Differentiating (4.5) with respect to γ and denoting $\frac{\partial}{\partial\gamma} = '$, we have

$$\lambda_1'(d_1, d_2, q_0, g, \gamma) + \frac{\partial\lambda_1(d_1, d_2, q_0, g, \gamma)}{\partial q_0} \cdot q_0' = 0,$$

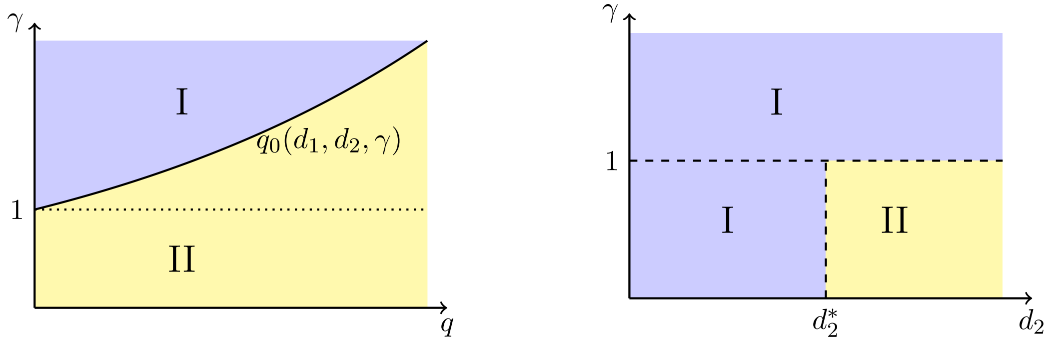
then $q_0' > 0$ by Lemma 4.2(i)(iii). Thus, by the implicit function theorem, $q_0(d_1, d_2, \gamma)$ is strictly increasing with respect to γ in $(1, +\infty)$. Note that $\lambda_1(d_1, d_2, 0, g, 1) = 0$ (see Lemma 4.2(i)) and

$$\lambda_1(d_1, d_2, q_0(d_1, d_2, 1), g, 1) = 0,$$

then $q_0(d_1, d_2, 1) = 0$. □

Remark 4.1. Theorem 4.1 reveals a fundamental tradeoff between physiological efficiency γ and hydrodynamic transport q when the effect of advection is stronger than the boundary reaction term of algae species:

- **(i)** Low efficiency (i.e., $\gamma \leq 1$): Mussel populations cannot establish regardless of flow conditions. In other words, the mussels cannot invade no matter how the advection of algae q changes.
- **(ii)** High efficiency (i.e., $\gamma > 1$): Slow flows (i.e., $q < q_0$) enables mussel persistence, while fast flows ($q > q_0$) leads to washout. The critical flow speed q_0 increases with γ, showing that more efficient consumers can persist under stronger advection.



(a) (b)

Fig. 3. Dynamical regimes characterized by Theorems 4.1 (left panel) and 4.2 (right panel). (I) Coexistence regime: The semi-trivial solution $(u^*(d_1,q,g),0)$ becomes unstable, allowing for a positive steady state (mussel-algae coexistence) (II) Extinction regime: $(u^*(d_1,q,g),0)$ is globally asymptotically stable (mussel extinction).

Fig. 3(a) provides a schematic representation of the key conclusions derived from Theorem 4.1.

4.2. Combined effects of growth rate, diffusion, and boundary conditions

To investigate how the interaction between energy conversion efficiency γ, mussel dispersal rate d_2, and boundary loss g influences the system dynamics when boundary effects dominate advection (i.e., $|g(u)| > q$), we first consider a simplified case with constant boundary flux $g(u) = b \le 0$, where $-b$ represents the relative loss rate at $x = L$ [12]. In this case, the system reduces to

$$\begin{cases} u_t = d_1 u_{xx} - q u_x + a(1-u) - uv, & 0<x<L, t>0,\\ v_t = d_2 v_{xx} + \gamma uv - \dfrac{v}{1+v}, & 0<x<L, t>0,\\ d_1 u_x(0,t) - qu(0,t) = 0, & t>0,\\ d_1 u_x(L,t) - qu(L,t) = bu(L,t), & t>0,\\ v_x(0,t) = v_x(L,t) = 0, & t>0,\\ u(x,0) = \varphi_1(x) \ge 0, \not\equiv 0, \quad v(x,0) = \varphi_2(x) \ge 0, \not\equiv 0, & 0 \le x \le L. \end{cases} \tag{4.6}$$

According to Theorem 3.1, there exists a unique semi-trivial steady state $(u^*(d_1,q,b),0)$ for system (4.6). And from Section 3.3, the eigenvalue problem obtained by linearizing the system (4.6) at the semi-trivial solution $(u^*(d_1,q,b),0)$ has principal eigenvalue $\lambda_1(d_1,d_2,q,b,\gamma)$.

From Proposition 3.2 and Lemma 4.2, it is easy to obtain the following lemma.

Lemma 4.3. *Suppose that $d_1,d_2,a,\gamma > 0$ and $q > 0$. Then the following statements hold.*

(i) *The algal steady state $u^*(d_1,q,b)$ is increasing in b on $[0,L]$.*

(ii) *The principal eigenvalue $\lambda_1(d_1,d_2,q,b,\gamma)$ is non-decreasing with respect to b in $(-\infty,0]$.*

Lemma 4.4. *The following statements on the principal eigenvalue $\lambda_1(d_1,d_2,q,b,\gamma)$ are true.*

(i) *If $\gamma > 1$, then there exists $b^* \le 0$, such that when $-q > b \ge b^*$, $\lambda_1(d_1,d_2,q,b,\gamma) > 0$ for all $d_2 > 0$.*

(ii) *If $\gamma < 1$, then for any b there exists a threshold value $d_2^* \in (0,\infty)$, such that $\lambda_1(d_1,d_2,q,b,\gamma) > 0$ (i.e., mussel invasion) for $0 < d_2 < d_2^*$, and $\lambda_1(d_1,d_2,q,b,\gamma) < 0$ (i.e., mussel extinction) for $d_2 > d_2^*$.*

Proof. Consider the following algae-only system:

$$\begin{cases} d_1 u_{xx} - q u_x + a(1-u) = 0, \quad 0<x<L,\\ d_1 u_x(0) - qu(0) = 0,\\ d_1 u_x(L) - qu(L) = bu(L). \end{cases} \tag{4.7}$$

According to Theorem 3.1, there exists a unique positive solution $u^*(d_1,q,b)$ for system (4.7). Integrating (4.7) over $(0,L)$, we have

$$\int_0^L u^*(d_1,q,b)(x)\mathrm{d}x = \frac{bu^*(d_1,q,b)(L) + aL}{a}.$$

For the eigenvalue problem (3.16) with $g(u) = b$ under the Neumann boundary conditions, in view of the threshold results of Theorem 2 in [45], we have

(a) If $\int_0^L (\gamma u^*(d_1,q,b)(x) - 1)\mathrm{d}x > 0$, then $\lambda_1(d_1,d_2,q,b,\gamma) > 0$ for all $d_2 > 0$;

(b) If $\int_0^L (\gamma u^*(d_1,q,b)(x) - 1)\mathrm{d}x < 0$, then there exists a threshold value $d_2^* \in (0,\infty)$, such that $\lambda_1(d_1,d_2,q,b,\gamma) > 0$ for $0 < d_2 < d_2^*$, and $\lambda_1(d_1,d_2,q,b,\gamma) < 0$ for $d_2 > d_2^*$.

Note that when $b = -q$, (4.7) can be transformed into an algae model with Danckwerts boundary conditions, which was studied in the [22]. It follows from Lemma 3.2 in [22] that $0 < u^*(d_1,q,-q)(x) < 1$ in $(0,L)$. Note that $u^*(d_1,q,b)(x)$ depends continuously and differentially on x, then by Lemma 4.3(i), we have $u^*(d_1,q,b)(L) < 1$ for $b < -q$. Thus,

$$\int_0^L u^*(d_1,q,b)(x)\mathrm{d}x = \frac{bu^*(d_1,q,b)(L) + aL}{a} \ge \frac{b}{a} + L.$$

If $\gamma > 1$, there exists $b^* \le 0$, such that $b^*\gamma + L(\gamma - 1) = 0$ and so

$$\int_0^L (\gamma u^*(d_1,q,b)(x) - 1)\mathrm{d}x \ge \gamma\frac{b}{a} + L(\gamma-1) > 0 \quad \text{for} \quad b \in (b^*,-q),$$

which together with Lemma 4.3(ii) implies that $\lambda_1(d_1,d_2,q,b,\gamma) > 0$ for all $d_2 > 0$ and $b \in (b^*,-q)$. Thus, the proof for conclusion (i) is completed.

Next, we show (ii). Note that

$$\int_0^L u^*(d_1,q,b)(x)\mathrm{d}x = \frac{bu^*(d_1,q,b)(L) + aL}{a} \le L.$$

If $\gamma < 1$, we have

$$\int_0^L (\gamma u^*(d_1,q,b)(x) - 1)\mathrm{d}x \le L(\gamma - 1) < 0.$$

Then there exists a threshold value $d_2^* \in (0,\infty)$, such that $\lambda_1(d_1,d_2,q,b,\gamma) > 0$ for $0 < d_2 < d_2^*$, and $\lambda_1(d_1,d_2,q,b,\gamma) < 0$ for $d_2 > d_2^*$. Thus, the proof for conclusion (ii) is completed. ☐

Based on the parameters range in Lemma 4.4, we have the following dynamic results of system (1.1).

Theorem 4.2. *Under conditions* (H1) *and* (H2)*, the following statements hold.*

- **(i)** *If $\gamma > 1$ (i.e., high conversion), then there exists $b^* \leq 0$, such that for any $d_2 > 0$, $(u^*(d_1, q, g), 0)$ is unstable when $-q > g(u) \geq b^*$ for all $u \in \mathbb{R}_+$.*
- **(ii)** *If $\gamma < 1$ (i.e., low conversion), then there exists a threshold value $d_2^* \in (0, \infty)$, such that $(u^*(d_1, q, g), 0)$ is unstable for $0 < d_2 < d_2^*$, and $(u^*(d_1, q, g), 0)$ is globally asymptotically stable for $d_2 > d_2^*$.*

Proof. The stability and instability of $(u^*(d_1, q, g), 0)$ follow from Proposition 3.3, and Theorem 3.3 indicates the global asymptotic stability of system (1.1). ☐

Remark 4.2. Theorem 4.2 reveals the combined effects of the conversion rate γ, mussel diffusion rate d_2, and the nonlinear boundary function g on the global dynamical behavior of system (1.1). More precisely, high energy conversion efficiency (i.e., $\gamma > 1$) leads to successful invasion when the boundary reaction effect of the algal species dominates advection, allowing mussels and algae to coexist. In contrast, when the conversion efficiency is low (i.e., $\gamma < 1$), mussels cannot successfully invade if their diffusion rate is large, regardless of how the boundary reaction term changes. In this case, mussels go extinct and only algae persist. However, mussel invasion becomes possible if they disperse slowly. Thus, Theorem 4.2 quantifies how boundary conditions mediate the interplay between the physiological factor γ and the ecological factor d_2 in determining the community structure. Fig. 3(b) provides a schematic summary of these dynamical regimes.

5. Existence of coexistence steady states

In this section, we employ bifurcation theory to establish the existence of positive steady-state solutions for system (1.1). These solutions bifurcate from the semi-trivial steady state $(u^*(d_1, q, g), 0)$ at critical parameter values where the principal eigenvalue $\lambda_1(d_1, d_2, q, g, \gamma) = 0$. The steady states satisfy the coupled elliptic system:

$$\begin{cases} d_1 u_{xx} - q u_x + a(1-u) - uv = 0, & 0 < x < L, \\ d_2 v_{xx} + \gamma uv - \dfrac{v}{1+v} = 0, & 0 < x < L, \\ d_1 u_x(0) - q u(0) = 0, \\ d_1 u_x(L) - q u(L) = u(L) g(u(L)), \\ v_x(0) = v_x(L) = 0. \end{cases} \tag{5.1}$$

Before proceeding with the bifurcation analysis, we first establish uniform bounds for potential solutions of (5.1).

Lemma 5.1 (*Solution Bounds*)**.** *Under assumption* (H1)*, for $d_1, d_2, a, \gamma, q > 0$, suppose that $(u(x), v(x))$ is a nonnegative solution of* (5.1) *with $u \not\equiv 0$ and $v \not\equiv 0$. Then*

$$0 < u(x) \leq K(x), \quad \forall x \in [0, L],$$

where $K(x)$ satisfies

$$K(x) = \frac{q + \alpha\left[L - \frac{d_1}{q}\left(1 - \exp\left\{-\frac{q}{d_1}L\right\}\right)\right]}{d_1\left(1 - \exp\left\{-\frac{q}{d_1}L\right\}\right)} L \exp\left\{-\frac{q}{d_1}(L-x)\right\} + \frac{\alpha L}{q}\left[1 - \exp\left\{-\frac{q}{d_1}(L-x)\right\}\right]$$

and when $\gamma a < 1$, there exists a positive constant C depending only on γ, d_2 and L, such that $v(x)$ satisfies

$$0 < v(x) \leq C, \quad \forall x \in [0, L].$$

The proof of Lemma 5.1 follows from adaptations of Lemmas 5.1–5.2 in [35], modified to account for the nonlinear boundary conditions specific to our setting. For brevity, the complete proof is omitted.

In what follows, we focus on the biologically relevant case where the energy conversion efficiency is high (i.e., $\gamma > 1$) and boundary losses are limited (i.e., $g(u) \geq -q$). Using the advection rate q as a bifurcation parameter, we analyze solutions branching from the semi-trivial solution curve $\Gamma_u = \{(q, u^*, 0) : q \in [0, +\infty)\}$. Here and throughout, we write $u^*(d_1, q, g)$ simply as u^* for convenience. Let $\mathbb{X} = W^{2,p}(0, L) \times W^{2,p}(0, L)$ and $\mathbb{Y} = L^p(0, L) \times L^p(0, L)$ with $p > 1$. Define a nonlinear mapping T: $\mathbb{R}_+ \times \mathbb{X} \to \mathbb{Y} \times \mathbb{R}_4$ by

$$T(q, u, v) = \begin{pmatrix} d_1 u_{xx} - q u_x + a(1-u) - uv \\ d_2 v_{xx} + \gamma uv - \frac{v}{1+v} \\ d_1 u_x(0) - q u(0) \\ v_x(0) \\ d_1 u_x(L) - q u(L) - u(L) g(u(L)) \\ v_x(L) \end{pmatrix}.$$

Hence the Fréchet derivative $D_{(u,v)}T(q, u, v)$ of $T(q, u, v)$ with respect to (u, v) at (u, v) is given by

$$D_{(u,v)}T(q, u, v)(\phi, \psi) = \begin{pmatrix} d_1 \phi_{xx} - q\phi_x - a\phi - u\psi - v\phi \\ d_2 \psi_{xx} + \gamma v\phi + (\gamma u - \frac{1}{(1+v)^2})\psi \\ d_1 \phi_x(0) - q\phi(0) \\ \psi_x(0) \\ d_1 \phi_x(L) - [q + g(u(L)) + u(L) g'(u(L))]\phi(L) \\ \psi_x(L) \end{pmatrix}. \tag{5.2}$$

It is easy to find that

(i) T is a continuously differentiable mapping on an open subset V of $\mathbb{R}_+ \times \mathbb{X}$;

(ii) $T(q, u^*, 0) = 0$ for all $q > 0$;

(iii) For any fixed $(q, u, v) \in \mathbb{R}_+ \times \mathbb{X}$, $D_{(u,v)}T(q, u, v)$ is a Fredholm operator with index zero (which follows from Remark 2.5 and Corollary 2.11 of [46]).

It follows from (4.5) that $\lambda_1(d_1, d_2, q_0, g, \gamma) = 0$ and that the kernel of $D_{(u,v)}T(q_0, u^*, 0)$ is

$$\mathcal{N}(D_{(u,v)}T(q_0, u^*, 0)) = \mathrm{span}\{(\phi_0, \psi_0)\},$$

where ψ_0 is a positive principal eigenfunction of the eigenvalue problem (3.16) with $q = q_0$, and ϕ_0 is the unique solution to the following system

$$\begin{cases} d_1 \phi_{xx} - q\phi_x - a\phi - u^*(d_1, q_0, g)\psi_0 = 0, & 0 < x < L, \\ d_1 \phi_x(0) - q\phi(0) = 0, \\ d_1 \phi_x(L) - q\phi(L) = \phi(L)[g(u^*(d_1, q_0, g)(L)) \\ \quad + u^*(d_1, q_0, g)(L) g'(u^*(d_1, q_0, g)(L))]. \end{cases}$$

Note that the principal eigenvalue λ_1^{ϕ} of (3.15) is negative (see (3.17)). By the general maximum principle, it follows that $\phi_0 < 0$, which implies that the algal component decreases as mussel populations emerge. Consequently, the coexistence solutions are biologically meaningful, as both components remain positive. Thus, we obtain the following result.

Lemma 5.2.

- **(i)** $\dim \mathcal{N}(D_{(u,v)}T(q_0, u^*, 0)) = 1$;
- **(ii)** $D_{q(u,v)}T(q_0, u^*, 0)(\phi_0, \psi_0)^T \notin \mathcal{R}(D_{(u,v)}T(q_0, u^*, 0))$.

Proof. We have proved the first assertion, that is, the kernel space of $D_{(u,v)}T(q_0, u^*, 0)$ is one-dimensional. Now, we shall prove assertion (ii). We first claim that the range of $D_{(u,v)}T(q, u^*, 0)$ is

$$\mathcal{R}(\mathrm{D}_{(u,v)}T(q_0, u^*, 0)) = \{(u, v, \xi_1, \xi_2, \xi_3, \xi_4) \in \mathbb{Y} \times \mathbb{R}_4 : l(u, v, \xi_1, \xi_2, \xi_3, \xi_4) = 0\},$$

where l: $\mathbb{Y}\times\mathbb{R}_4 \to \mathbb{R}$ is a linear functional in $(\mathbb{Y}\times\mathbb{R}_4)^*$ defined by

$$l(u,v,\xi_1,\xi_2,\xi_3,\xi_4) = \int_0^L \psi_0 v \mathrm{d}x + d_2\xi_2\psi_0(0) - d_2\xi_4\psi_0(L).$$

To prove this, suppose $(u,v,\xi_1,\xi_2,\xi_3,\xi_4) \in \mathcal{R}(D_{(u,v)}T(q_0,u^*,0))$. Then there exists $(\phi,\psi)\in\mathbb{X}$ such that

$$\begin{cases} d_1\phi_{xx} - q\phi_x - a\phi - u^*(d_1,q_0,g)\psi = u, & 0<x<L,\\ d_2\psi_{xx} + [\gamma u^*(d_1,q_0,g)-1]\psi = v, & 0<x<L,\\ d_1\phi_x(0) - q\phi(0) = \xi_1, \\ d_1\phi_x(L) - [q + g(u^*(d_1,q_0,g)(L)) + u^*(d_1,q_0,g)(L)g'(u^*(d_1,q_0,g)(L))]\phi(L) = \xi_3, \\ \psi_x(0) = \xi_2, \quad \psi_x(L) = \xi_4. \end{cases} \tag{5.3}$$

Note that

$$\begin{cases} d_2(\psi_0)_{xx} + [\gamma u^*(d_1,q_0,g)-1]\psi_0 = 0, & 0<x<L,\\ (\psi_0)_x(0) = 0, \quad (\psi_0)_x(L) = 0. \end{cases} \tag{5.4}$$

Multiplying the second equation of (5.3) by ψ_0 and the first equation of (5.4) by ψ, integrating over $(0,L)$ by parts and subtracting, we obtain

$$\int_0^L \psi_0 v \mathrm{d}x + d_2\xi_2\psi_0(0) - d_2\xi_4\psi_0(L) = 0.$$

Since all eigenvalues of (3.15) are negative (see (3.17)), then by Fredholm alternative theorem, we conclude that the following system

$$\begin{cases} d_1\phi_{xx} - q\phi_x - a\phi - u^*(d_1,q_0,g)\psi = u, & 0<x<L,\\ d_1\phi_x(0) - q\phi(0) = \xi_1, \\ d_1\phi_x(L) - [q + g(u^*(d_1,q_0,g)(L)) \\ \quad + u^*(d_1,q_0,g)(L)g'(u^*(d_1,q_0,g)(L))]\phi(L) = \xi_3 \end{cases} \tag{5.5}$$

always has a unique solution ϕ in $W^{2,p}(0,L)$ for any $u\in L^p(0,L)$ and $\xi_1,\xi_3\in\mathbb{R}$. Hence, $(u,v,\xi_1,\xi_2,\xi_3,\xi_4)\in\mathcal{R}(D_{(u,v)}T(q_0,u^*,0))$ if and only if $\int_0^L \psi_0 v \mathrm{d}x + d_2\xi_2\psi_0(0) - d_2\xi_4\psi_0(L) = 0$.

Next, we apply the bifurcation theorem from a simple eigenvalue established by Crandall and Rabinowitz [47], we need to check the transversality condition $D_{q(u,v)}T(q_0,u^*,0)(\phi_0,\psi_0)^T \notin \mathcal{R}(D_{(u,v)}T(q_0,u^*,0))$. Differentiating (5.2) with respect to q, we obtain

$$D_{q(u,v)}T(q_0,u^*,0)(\phi_0,\psi_0) = \\ \begin{pmatrix} -(\phi_0)_x - \left.\frac{\partial u^*}{\partial q}\right|_{q=q_0}\psi_0 \\ \gamma\left.\frac{\partial u^*}{\partial q}\right|_{q=q_0}\psi_0 \\ -\phi_0(0) \\ 0 \\ -\phi_0(L)\left[1 + \left.\left(\frac{\partial g}{\partial q}\cdot\frac{\partial u^*}{\partial q}\right)\right|_{q=q_0} + \left.\left(\frac{\partial u^*}{\partial q}g'(u^*) + u^*\frac{\partial g'}{\partial q}\cdot\frac{\partial u^*}{\partial q}\right)\right|_{q=q_0}\right] \\ 0 \end{pmatrix}$$

and

$$l(D_{q(u,v)}T(q_0,u^*,0)(\phi_0,\psi_0)^T) = \int_0^L \psi_0^2\gamma\left.\frac{\partial u^*}{\partial q}\right|_{q=q_0}\mathrm{d}x < 0$$

due to $\left.\frac{\partial u^*}{\partial q}\right|_{q=q_0} < 0$ in $(0,L)$ (see Proposition 3.1 (iii)). Hence,

$$D_{q(u,v)}T(q_0,u^*,0)(\phi_0,\psi_0)^T \notin \mathcal{R}(D_{(u,v)}T(q_0,u^*,0)).$$

The proof is completed. □

Lemma 5.2 provides the necessary conditions for applying standard bifurcation theory [47], ensuring the existence of coexistence solutions in a neighborhood of $(q_0,u^*,0)$. To fully characterize the bifurcation structure, we now examine the complementary subspace of $\mathrm{span}\{(\phi_0,\psi_0)\}$ in $\mathbb{X}$, which plays a critical role in determining the local structure of the solution branch.

Lemma 5.3. *$\mathrm{span}\{(\phi_0,\psi_0)\}\oplus\mathbb{U} = \mathbb{X}$, where*

$$\mathbb{U} = \left\{(u,v)\in\mathbb{X} : \int_0^L \psi_0 v \mathrm{d}x = 0\right\}.$$

Proof. We cannot work directly on the operator T because $D_{(u,v)}T(q,u,v)$ is not self-adjoint. As stated in Section 2, we may set $\tilde{u}(x) = u(x)e^{-\beta x}$ and consider the modified operator $\tilde{T}$: $\mathbb{R}_+\times\mathbb{X}\to\mathbb{Y}\times\mathbb{R}_4$ by

$$\widetilde{T}(q,u,v) = \begin{pmatrix} d_1u_{xx} + qu_x + a(e^{-\beta x} - u) - uv \\ d_2v_{xx} + \gamma e^{\beta x}uv - \frac{v}{1+v} \\ d_1u_x(0) \\ d_2v_x(0) \\ d_1u_x(L) - u(L)g(e^{\beta L}u(L)) \\ d_2v_x(L) \end{pmatrix}.$$

Hence the Fréchet derivative $D_{(u,v)}\tilde{T}(q,u,v)$ of $\tilde{T}(q,u,v)$ with respect to (u,v) at $(q_0,\tilde{u}^*,0)$ is given by

$$D_{(u,v)}\tilde{T}(q_0,\tilde{u}^*,0)(\phi,\psi) = \begin{pmatrix} d_1\phi_{xx} + q\phi_x - a\phi - \tilde{u}^*\psi \\ d_2\psi_{xx} + (\gamma u^* - 1)\psi \\ d_1\phi_x(0) \\ d_2\psi_x(0) \\ d_1\phi_x(L) - [g(u^*(L)) + u^*(L)g'(u^*(L))]\phi(L) \\ d_2\psi_x(L) \end{pmatrix}.$$

Similarly to the previous discussion, we have

$$\mathcal{N}(D_{(u,v)}\tilde{T}(q_0,\tilde{u}^*,0)) = \mathrm{span}\{(\phi_0e^{-\beta(\cdot)},\psi_0)\}.$$

Let the duality $\langle\cdot,\cdot\rangle$: $\mathbb{X}\times(\mathbb{Y}\times\mathbb{R}_4)\mapsto\mathbb{R}$ between $\mathbb{X}$ and $\mathbb{Y}\times\mathbb{R}_4$ be defined as

$$\begin{aligned}\langle\Psi,(\Phi,\xi)\rangle &= \int_0^L e^{\beta x}\psi_1(x)\varphi_1(x)\mathrm{d}x + \psi_1(0)\xi_1 - e^{\beta L}\psi_1(L)\xi_3 \\ &\quad + \int_0^L \psi_2(x)\varphi_2(x)\mathrm{d}x + \psi_2(0)\xi_2 - \psi_2(L)\xi_4\end{aligned}$$

for all $\Psi = (\psi_1,\psi_2)\in\mathbb{X}$, $\Phi = (\varphi_1,\varphi_2)\in\mathbb{Y}$, and $\xi = (\xi_1,\xi_2,\xi_3,\xi_4)\in\mathbb{R}_4$. Then we have

$$\langle\Psi, D_{(u,v)}\tilde{T}(q_0,\tilde{u}^*,0)\Phi\rangle = \langle\Phi,\mathcal{L}^*\Psi\rangle,$$

where

$$\mathcal{L}^*(\phi,\psi) = \begin{pmatrix} d_1\phi_{xx} + q\phi_x - a\phi \\ d_2\psi_{xx} + (\gamma u^* - 1)\psi - u^*\phi \\ d_1\phi_x(0) \\ d_2\psi_x(0) \\ d_1\phi_x(L) - [g(u^*(L)) + u^*(L)g'(u^*(L))]\phi(L) \\ d_2\psi_x(L) \end{pmatrix}.$$

Thus, we have $\mathcal{N}(\mathcal{L}^*) = \mathrm{span}\{(0,\psi_0)\}$ and so $\mathbb{U} = \{(u,v)\in\mathbb{X} : \int_0^L \psi_0 v \mathrm{d}x = 0\}$ is complement of $\mathrm{span}\{(\phi_0,\psi_0)\}$ in $\mathbb{X}$, that is, $\mathrm{span}\{(\phi_0,\psi_0)\}\oplus\mathbb{U} = \mathbb{X}$. The proof is completed. □

We now present our main existence result using global bifurcation theory [46]. The following theorem establishes conditions for the existence of coexistence solutions to system (5.1).

Theorem 5.1. *Suppose that $\gamma > 1$ and $g(u) \geq -q$ for all $u\in\mathbb{R}$. Then system (5.1) admits at least one positive solution for all advection rates $0\leq q<q_0$.*

Proof. In view of Lemma 5.2, we see that $(q_0,u^*,0)$ is a bifurcation point. By Theorem 1.7 in [47] or Theorem 4.3 in [46], there exists a $\varepsilon>0$ and C^1 curve $(q(s),u(s),v(s)) : (-\varepsilon,\varepsilon)\mapsto\mathbb{R}\times\mathbb{X}$ defined by

$$(q(s),u(s),v(s)) = (q(s),u^* + s(\phi_0 + \Phi(s)), s(\psi_0 + \Psi(s))),$$

such that $T(q(s),u(s),v(s)) = 0$, where $q(0) = q_0, \Phi(0) = 0, \Psi(0) = 0, (\Phi(s),\Psi(s))\in\mathbb{U}$. We are interested in the branch of positive solutions, that is, $\Gamma_1^+ = \{(q(s),u(s),v(s)) : 0<s<\varepsilon\}$ is exactly the positive solution branch of (5.1) near the bifurcation point $(q_0,u^*,0)$. By Theorem 4.3 and Theorem 4.4 in [46] for Fredholm operators, we may extend the local solution branch Γ_1^+ to a global one.

By Theorem 4.3 in [46], we obtain a connected component C of the set

$$\{(q,u,v)\in\mathbb{R}_+\times\mathbb{X} : T(q,u,v) = 0, (u,v)\neq(u^*,0)\}$$

from Γ_u at $(q_0, u^*, 0)$. Moreover, either $\mathcal{C}$ is not compact in $\mathbb{R}_+ \times \mathbb{X}$ or $\mathcal{C}$ contains a point $(q_1, u^*, 0)$ with $q_1 \neq q_0$. Clearly, $\Gamma_1^+ \subset \mathcal{C}$. Let $\mathbb{X}_+ = \{(u,v) \in \mathbb{X} : u > 0, v > 0 \text{ on } [0,L]\}$. Then $\mathcal{C} \cap (\mathbb{R}_+ \times \mathbb{X}_+) \neq \emptyset$.

Let $\Gamma = \mathcal{C} \cap (\mathbb{R}_+ \times \mathbb{X}_+)$. Then Γ consists of the local positive solution branch Γ_1^+ near the bifurcation point $(q_0, u^*, 0)$. Let $\mathcal{C}^+$ be the connected component of $\mathcal{C} \setminus \{(q(s), u(s), v(s)) : s \in (-\varepsilon, 0)\}$. Then $\Gamma \subset \mathcal{C}^+$. It follows from Theorem 4.4 in [46] that $\mathcal{C}^+$ satisfies one of the following alternatives:

(i) $\mathcal{C}^+$ is not compact;

(ii) $\mathcal{C}^+$ contains a point $(q^*, u^*, 0)$ for some $q^* \neq q_0$;

(iii) $\mathcal{C}^+$ contains a point $(q, u^* + u, v)$ for some $(u,v) \in \mathbb{U}$ and $(u,v) \neq (0,0)$.

Suppose alternative (ii) holds. Then we can find a sequence of points $(q_n, u_n, v_n) \subset \Gamma \cap (\mathbb{R}_+ \times \mathbb{X}_+)$, which converges to $(q^*, u^*, 0)$ in $\mathbb{R}_+ \times \mathbb{X}_+$. It follows from the equation for v_n that we have $\mu_1(d_2, \gamma u_n^* - \frac{1}{1+v_n}) = 0$. It follows from Lemma 4.1 (ii) that $\mu_1\left(d_2, \gamma u^* - 1\right) = 0$ by letting $n \to +\infty$. That is, $\lambda_1(d_1, d_2, q^*, g, \gamma) = 0$. By Eq. (4.5), one can conclude that $q^* = q_0$. Thus, alternative (ii) cannot occur.

Suppose alternative (iii) holds. For any $(q, u^* + u, v) \in \Gamma$, we have $v > 0$ on $[0,L]$. Thus, $\int_0^L \psi_0 v \mathrm{d}x > 0$, which contradicts $(u,v) \in \mathbb{U}$. Hence, alternative (iii) cannot occur.

It follows from Lemma 5.1 and Theorem 4.1 that every positive solution of (5.1) satisfies $0 < u < K(x)$, $0 < v < C$, $0 \leq q < q_0$. Integrating the first and second equations of (5.1) from 0 to x, we conclude that u_x and v_x are uniformly bounded in $(0,L)$. It follows from (5.1) that u_{xx} and v_{xx} are uniformly bounded in $(0,L)$. Hence, positive solutions of (5.1) must be bounded in $\mathbb{X}$. Thus, assertion (i) implies that $\Gamma - \{(q_0, u^*, 0)\} \not\subset \mathbb{R}_+ \times \mathbb{X}_+$. Thus, there exists a sequence $\{(q_n, u_n, v_n)\} \subset \Gamma \cap (\mathbb{R}_+ \times \mathbb{X}_+)$ with $u_n, v_n > 0$ on $[0,L]$, which converges to $(\bar{q}, \bar{u}, \bar{v})$, where $(\bar{q}, \bar{u}, \bar{v}) \in (\Gamma - \{(q_0, u^*, 0)\}) \cap \partial(\mathbb{R}_+ \times \mathbb{X}_+)$. It follows from $(\bar{q}, \bar{u}, \bar{v}) \in \partial(\mathbb{R}_+ \times \mathbb{X}_+)$ that one of the following alternatives holds:

(a) $\bar{u} \geq 0$, and $\bar{u}(x_0) = 0$ for some point $x_0 \in [0,L]$;

(b) $\bar{v} \geq 0$, and $\bar{v}(x_0) = 0$ for some point $x_0 \in [0,L]$;

(c) $\bar{q} = 0$.

By the strong maximum principle, one can obtain that $\bar{u} > 0$ on $[0,L]$, thus (a) is impossible.

If (b) holds, the strong maximum principle leads to $\bar{v} \equiv 0$. Thus, we obtain $(\bar{u}, \bar{v}) \equiv (u^*, 0)$ and hence the sequence (q_n, u_n, v_n) satisfies that $q_n \to \bar{q}$ and $(u_n, v_n) \to (u^*, 0)$ in $\mathbb{X}$ as $n \to \infty$. It follows from the equation of v_n again that

$$\mu_1\left(d_2, \gamma u_n^* - \frac{1}{1+v_n}\right) = 0.$$

Letting $n \to +\infty$, we get $\mu_1\left(d_2, \gamma u^* - 1\right) = 0$ by Lemma 4.1 (ii). That is, $\lambda_1(d_1, d_2, \bar{q}, g, \gamma) = 0$. In view of (4.5), we conclude that $\bar{q} = q_0$, a contradiction.

Hence, (c) must hold. Namely, there exist $q_n \to 0$ and positive solutions $(\bar{u}, \bar{v})$ of system (5.1) with $q = q_n$ such that $(q_n, u_n, v_n) \to (0, \bar{u}, \bar{v})$ in $\mathbb{X}$ as $n \to +\infty$. Integrating the equations for u_n and v_n from 0 to x, respectively, one can conclude that $(u_n)_x$ and $(v_n)_x$ are uniformly bounded in $[0,L]$. Hence, we see that $(u_n)_{xx}$ and $(v_n)_{xx}$ are uniformly bounded in $[0,L]$ by using the equations for u_n and v_n respectively again. Passing to a subsequence if necessary, we may assume that $(u_n, v_n) \to (\bar{u}, \bar{v})$ in $C^1[0,L] \times C^1[0,L]$. Moreover, it is easy to see $(\bar{u}, \bar{v})$ fulfills system (5.1) with $q = 0$. Next, we show $\bar{u}, \bar{v} > 0$ on $[0,L]$. Clearly, $\bar{u} > 0$ on $[0,L]$ by applying the strong maximum principle to the equation of $\bar{u}$ (or see Lemma 5.1). If $\bar{v}(x_0) = 0$ for some point $x_0 \in [0,L]$, then the strong maximum principle leads to $\bar{v} \equiv 0$ on $[0,L]$, which implies $\bar{u} = u^*$. That is, $(\bar{u}, \bar{v}) \to (u^*, 0)$ in $\mathbb{X}$ as $n \to \infty$. By the similar arguments used to eliminate alternative (b), we can obtain $\mu_1(d_2, \gamma u^* - 1) = 0$ for $q = 0$, a contradiction to (4.5). Therefore, we have $\bar{u}, \bar{v} > 0$ on $[0,L]$. Now, we can conclude that the global bifurcation branch Γ must intersect with the branch $\{(0,u,v) : u, v > 0\}$ at the point $(0, \bar{u}, \bar{v})$ as $q \to 0$. The proof is completed. □

6. Discussion

In this paper, we investigated a reaction–diffusion–advection system modeling consumer-resource interactions between stationary mussels and their drifting algal food source, incorporating biologically motivated nonlinear boundary conditions. Our analysis revealed several significant theoretical findings. The introduction of nonlinear boundary fluxes creates a mathematically richer and biologically more realistic framework, fundamentally altering the system's qualitative behavior. Unlike classical models with homogeneous boundary conditions, system (1.1) admits neither trivial nor spatially constant steady states. This crucial distinction renders classical linearization and eigenvalue-based approaches inapplicable for analyzing semi-trivial steady states. To address this, we developed a non-variational framework based on carefully constructed super- and sub-solutions, which establishes the global existence of solutions, the existence and stability of semi-trivial steady states, and key qualitative properties of the system under nonlinear boundary constraints.

In addition to resolving well-posedness challenges posed by nonlinear boundaries, we identified and corrected certain technical limitations in earlier work by Qu et al. [35], particularly regarding solution properties. Our Proposition 3.1(iii) extends and generalizes results from Qu et al. [35] and Wang et al. [22], establishing a crucial connection between systems with linear boundary conditions and those governed by more realistic nonlinear fluxes. This bridge reinforces the robustness of our framework and highlights the novel theoretical insights gained by moving beyond linear boundary assumptions.

Furthermore, we examined the joint influence of advection and boundary reactions on system dynamics. We identified two distinct dynamical regimes depending on the relative magnitudes of the advection rate q and the boundary flux $g(u)$. In advection-dominated settings (i.e., $|g(u)| < q$), the positive steady-state solution for algae decreases monotonically with increasing flow, while under stronger boundary retention (i.e., $|g(u)| > q$), solutions exhibit increasing dependence on boundary effects. These findings reveal parameter sensitivities not fully captured in prior studies [22,35], providing a more complete theoretical characterization of transport-boundary coupling in consumer-resource systems.

A central contribution of this work is the derivation of precise threshold conditions governing the global extinction or persistence of the mussel population under assumptions (H1)–(H2). These thresholds are linked to the principal eigenvalue of an associated boundary value problem and depend intricately on model parameters, including algal and mussel diffusion coefficients (d_1, d_2), the energy conversion efficiency γ, the advection rate q, and the boundary reaction term $g(u)$. Theorem 4.1 yields a particularly sharp result: when advection dominates boundary effects ($q > |g(u)|$), low energy conversion efficiency (i.e., $\gamma \leq 1$) inevitably results in mussel extinction, regardless of flow velocity. This generalizes Theorem 4.3 in Wang et al. [22], which was restricted to the special case of free-flow boundaries ($g(u) = -q$).

A more comprehensive view of the systems long-term dynamics is provided by Theorem 4.2, which identifies multiple biologically meaningful regimes:

(i) **High conversion efficiency** ($\gamma > 1$): Mussel invasion and stable coexistence are possible when boundary retention exceeds advection, i.e., $|g(u)| > q$.

(ii) **Low conversion efficiency** ($\gamma \leq 1$): Mussel persistence depends on limited dispersal; large diffusion (d_2) leads to extinction, while persistence is attainable when mussel mobility is restricted (i.e., small d_2).

These results offer theoretical support for key ecological mechanisms: (i) the critical role of boundary retention in sustaining populations in flowing environments, (ii) the interaction of physiological traits (notably γ) with environmental transport processes, and (iii) the trade-off between dispersal and resource acquisition under advective constraints. Overall, our analysis highlights the ecological significance of nonlinear boundary effects, a feature largely unexplored in earlier models assuming homogeneous or linear boundary fluxes. These insights have practical implications for understanding population structure and management in rivers, estuaries, and other flow-dominated ecosystems.

While our work provides a detailed analytical framework for consumer-resource systems with nonlinear boundary conditions, several important challenges remain:

(i) Role of algal diffusion: The influence of the algal diffusion coefficient d_1 on global dynamics remains only partially understood. In the single-species algae model, nonlinear boundary conditions can induce non-monotonic dependence on d_1, arising from interactions between diffusion and nonlinear fluxes. A complete analytical characterization of this behavior remains a topic for future study.

(ii) Uniqueness and global stability: Although Theorem 5.1 establishes the existence of coexistence steady states via global bifurcation theory, the uniqueness and global stability of these solutions remain open. Classical techniques such as Lyapunov functionals and integral estimates [48] are inapplicable due to the non-Lotka–Volterra structure and the presence of nonlinear boundary terms. Novel techniques are needed to address these stability challenges.

(iii) Asymptotic diffusion limits: Investigating the asymptotic behavior of steady states as $d_1 \to 0$ (revealing boundary-layer phenomena) and $d_1 \to \infty$ (where homogenization effects may dominate) could provide further insight into the role of spatial heterogeneity in shaping ecological outcomes.

(iv) General boundary fluxes: The present analysis assumes that $g(u)$ is decreasing. It would be of theoretical and ecological interest to study cases where $g'(u) > 0$, or where g is non-monotone or piecewise-defined. Such generalizations may better reflect real-world ecological boundary interactions, though they introduce additional analytical complexity that would likely require new mathematical frameworks.

Addressing these open problems will require the development of new tools for analyzing nonlinear parabolic systems with complex boundary conditions. Future research in these directions promises both theoretical advances and practical relevance for understanding species persistence in flowing environments.

CRediT authorship contribution statement

Chaochao Li: Writing – original draft, Methodology, Investigation, Formal analysis. **Hao Wang:** Writing – review & editing. **Shangjiang Guo:** Writing – review & editing, Supervision.

Funding

The research of Shangjiang Guo was partially supported by the National Natural Science Foundation of P.R. China (Grant Nos. 12071446 and 12471173), and the Fundamental Research Funds for the Central Universities, China, China University of Geosciences (Wuhan) (Grant No. CUGST2). The research of Hao Wang was partially supported by the Natural Sciences and Engineering Research Council of Canada (Individual Discovery Grant RGPIN-2020-03911 and Discovery Accelerator Supplement Award, Canada RGPAS-2020-00090) and the Canada Research Chairs program (Tier 1 Canada Research Chair Award).

Declaration of competing interest

The authors (Chaochao Li, Hao Wang, Shangjiang Guo) declare that there is no conflict of interest regarding the publication of this paper.

Acknowledgments

The authors express their gratitude to Dr. Min Li at China University of Geosciences (Wuhan) for his kind help with numerical simulations in this paper. The authors would like to thank the reviewer and editor for their careful reading of the manuscript and helpful comments.

Data availability

No data was used for the research described in the article.

References

[1] F. Lutscher, R.M. Nisbet, E. Pachepsky, Population persistence in the face of advection, Theor. Ecol. 3 (2010) 271–284.
[2] F. Lutscher, E. Pachepsky, M.A. Lewis, The effect of dispersal patterns on stream populations, SIAM J. Appl. Math. 65 (2005) 1305–1327.
[3] D.C. Speirs, W.S.C. Gurney, Population persistence in rivers and estuaries, Ecology 82 (2001) 1219–1237.
[4] Y. Jin, R. Peng, J.P. Shi, Population dynamics in river networks, J. Nonlinear Sci. 29 (2019) 2501–2545.
[5] F. Lutscher, M.A. Lewis, E. McCauley, Effects of heterogeneity on spread and persistence in rivers, Bull. Math. Biol. 68 (2006) 2129–2160.
[6] D. Tang, P. Zhou, On a Lotka–Volterra competition-diffusion-advection system: homogeneity vs heterogeneity, J. Differential Equations 268 (2020) 1570–1599.
[7] Q. Huang, H. Wang, M.A. Lewis, A hybrid continuous/discrete-time model for invasion dynamics of zebra mussels in rivers, SIAM J. Appl. Math. 77 (2017) 854–880.
[8] Q. Huang, H. Wang, A. Ricciardi, M.A. Lewis, Temperature-and turbidity-dependent competitive interactions between invasive freshwater mussels, Bull. Math. Biol. 78 (2016) 353–380.
[9] K.Y. Lam, Y. Lou, F. Lutscher, Evolution of dispersal in closed advective environments, J. Biol. Dyn. 9 (2015) 188–212.
[10] Y. Lou, F. Lutscher, Evolution of dispersal in open advective environments, J. Math. Biol. 69 (6–7) (2014) 1319–1342.
[11] Y. Lou, D. Xiao, P. Zhou, Qualitative analysis for a Lotka–Volterra competition system in advective homogeneous environment, Discrete Contin. Dyn. Syst. 36 (2) (2016) 953–969.
[12] Y. Lou, P. Zhou, Evolution of dispersal in advective homogeneous environment: The effect of boundary conditions, J. Differential Equations 259 (2015) 141–171.
[13] F. Lutscher, E. McCauley, M.A. Lewis, Spatial patterns and coexistence mechanisms in systems with unidirectional flow, Theor. Popul. Biol. 71 (2007) 267–277.
[14] L. Ma, D. Tang, Evolution of dispersal in advective homogeneous environments, Discrete Contin. Dyn. Syst. 40 (2020) 5815–5830.
[15] P. Zhou, On a Lotka–Volterra competition system: diffusion vs advection, Calc. Var. Partial Differential Equations 55 (2016) 137.
[16] P. Zhou, X.Q. Zhao, Global dynamics of a two species competition model in open stream environments, J. Dynam. Differential Equations 30 (2018) 613–636.
[17] F.M. Hilker, M.A. Lewis, Predator-prey systems in streams and rivers, Theor. Ecol. 3 (2010) 175–193.
[18] Y. Lou, H. Nie, Global dynamics of a generalist predator–prey model in open advective environments, J. Math. Biol. 84 (2022) 46.
[19] H. Nie, B. Wang, J.H. Wu, Invasion analysis on a predator–prey system in open advective environments, J. Math. Biol. 81 (2020) 1429–1463.
[20] H. Nie, S.X. Xin, H.Y. Shu, Effects of diffusion and advection on predator–prey dynamics in closed environments, J. Differential Equations 367 (2023) 290–331.
[21] K. H. Wang, Y. Kuang Dunning, Daphnia species invasion, competitive exclusion, and chaotic coexistence, Discret. Cont. Dyn. B 12 (2009) 481–493.
[22] J.F. Wang, X. Tong, Y.L. Song, Dynamics and pattern formation in a reaction–diffusion-advection mussel-algae model, Z. Angew. Math. Phys. 73 (2022) 117.
[23] Y. Wang, J.P. Shi, J.F. Wang, Persistence and extinction of population in reaction–diffusion-advection model with strong Allee effect growth, J. Math. Biol. 78 (7) (2019) 2093–2140.
[24] M. Kuussaari, I. Saccheri, M. Camara, I. Hanski, Allee effect and population dynamics in the glanville fritillary butterfly, Oikos 82 (1998) 384–392.
[25] R.S. Cantrell, C. Cosner, On the effects of nonlinear boundary conditions in diffusive logistic equations on bounded domains, J. Differential Equations 231 (2006) 768–804.

[26] R.S. Cantrell, C. Cosner, Density dependent behavior at habitat boundaries and the Allee effect, Bull. Math. Biol. 69 (2007) 2339–2360.
[27] R.S. Cantrell, C. Cosner, S. Martínez, Global bifurcation of solutions to diffusive logistic equations on bounded domains subject to nonlinear boundary conditions, Proc. R. Soc. Edinb. Sect. A 139 (2009) 45–56.
[28] S.J. Guo, Bifurcation in a reaction–diffusion model with nonlocal delay effect and nonlinear boundary condition, J. Differential Equations 289 (2021) 236–278.
[29] S.J. Guo, Global dynamics of a Lotka–Volterra competition-diffusion system with nonlinear boundary conditions, J. Differential Equations 352 (2023) 308–353.
[30] S.J. Guo, Existence and stability of positive solutions in a parabolic problem with a nonlinear incoming flux on the boundary, J. Differential Equations 436 (2025) 113349.
[31] K.K. Liu, S.J. Guo, Bifurcation in a reaction–diffusion-advection equation with nonlinear boundary conditions, Int. J. Bifurc. Chaos 35 (07) (2025) 2550077.
[32] P. Liu, J. Shi, Bifurcation of positive solutions to scalar reaction–diffusion equations with nonlinear boundary condition, J. Differential Equations 264 (2018) 425–454.
[33] R.A. Cangelosi, D.J. Wollkind, B.J. Kealy-Dichone, I. Chaiya, Nonlinear stability analyses of turing patterns for a mussel-algae model, J. Math. Biol. 70 (2015) 1249–1294.
[34] Y.L. Song, H.P. Jiang, Q.X. Liu, Y. Yuan, Spatiotemporal dynamics of the diffusive mussel-algae model near Turing–Hopf bifurcation, SIAM J. Appl. Dyn. Syst. 16 (4) (2017) 2030–2062.
[35] A.Q. Qu, X. Tong, J.F. Wang, Dynamics of a diffusive mussel-algae system in closed advective environments, J. Differential Equations 370 (2023) 346–377.
[36] Z.L. Shen, J.J. Wei, Bifurcation analysis in a diffusive mussel-algae model with delay, Int. J. Bifurc. Chaos 29 (11) (2019) 1950144.
[37] Z.L. Shen, J.J. Wei, Spatiotemporal patterns in a delayed reaction–diffusion mussel-algae model, Int. J. Bifurc. Chaos 29 (12) (2019) 1950164.
[38] J.F. Wang, H. Nie, Invasion dynamics of a predator–prey system in closed advective environments, J. Differential Equations 318 (2022) 298–322.
[39] C.C. Li, S.J. Guo, Bifurcation and stability of a reaction–diffusion-advection model with nonlocal delay effect and nonlinear boundary condition, Nonlinear Anal. Real World Appl. 78 (2024) 104089.
[40] C.Y. Tian, S.J. Guo, Global dynamics of a Lotka–Volterra competition-diffusion system with advection and nonlinear boundary conditions, Z. Angew. Math. Phys. 75 (2024) 103.
[41] C.V. Pao, Nonlinear Parabolic and Elliptic Equations, Plenum Press, New York, 1992.
[42] J.K. Hale, Asymptotic Behavior of Dissipative Systems, in: Math. Surveys Monogr., vol. 25, American Mathematical Society, Providence, 1988.
[43] X.Q. Zhao, Dynamical Systems in Population Biology, second ed., Springer, 2017.
[44] R.S. Cantrell, C. Cosner, Spatial Ecology Via Reaction-Diffusion Equations, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, Ltd., Chichester, 2003.
[45] L.J.S. Allen, B.M. Bolker, Y. Lou, A.L. Nevai, Asymptotic profiles of the steady states for an SIS epidemic reaction–diffusion model, Discrete Contin. Dyn. Syst. Ser. B 21 (2008) 1–20.
[46] J.P. Shi, X.F. Wang, On global bifurcation for quasilinear elliptic systems on bounded domains, J. Differential Equations 246 (7) (2009) 2788–2812.
[47] M.G. Crandall, P.H. Rabinowitz, Bifurcation from simple eigenvalues, J. Funct. Anal. 8 (1971) 321–340.
[48] W.J. Ni, J.P. Shi, M.X. Wang, Global stability of nonhomogeneous equilibrium solution for the diffusive competition model, Calc. Var. Partial Differential Equations 59 (2020) 132.