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A pivotal eigenvalue problem in river ecology ☆

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Abstract

This paper studies an eigenvalue problem associated with a linear parabolic equation and a coupled ordinary differential equation. The existence and the uniqueness of the principal eigenvalue for this eigenvalue problem is first established. Then, the qualitative dependence of the principal eigenvalue with respect to the several parameters involved in the system is analyzed. Finally, these results are applied to a system in flowing habitats with a hydraulic storage zone and light limitation.

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Keywords: Principal eigenvalue; Hydraulic storage zone; Light limitation; Steady states; Global attractivity; Uniform persistence

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1. Introduction

In this paper we focus our attention on the problem of analyzing the longitudinal distribution of the algae abundance in a riverine reservoir under various types of flows. Motivated by considering habitats as broad high-order rivers, or riverine reservoirs constructed by damming a river, we will propose a modification of the flow reactor model of Kung and Baltzis [17] to study this problem. It is well known that a rapid advective flow in these habitats can prevent persistence for realistic values of the parameters even of one single species. As a matter of fact, the presence of hydraulic storage zones in flowing water habitats might explain that persistence paradox [26]. Grover et al. [8] improved the original flow reactor model formulated by Kung and Baltzis [17] by adding a hydraulic storage zone with no spatial transport. Although the model of [8] is spatially heterogeneous, it is one-dimensional with a simple habitat geometry and transport processes. So, it is best suited for understanding longitudinal patterns along the flow axis. By using bifurcation theory as the main technical device, Grover et al. [8] successfully confirmed that a system with storage zones facilitates persistence of planktonic algae in flowing habitats.

The system of [8] is not only interesting biologically but also extremely challenging from the mathematical point of view, as some of its equations have no diffusion terms, while the remaining do, and hence, the associated Poincaré maps cannot be compact, which makes mathematics harder. By the lack of compactness of the associated solution operator, to get satisfactory results one should previously overcome two basic difficulties. The first one arises when establishing the existence of a "global compact attractor", as the classical Theorem 3.4.8 of Hale [10] cannot be applied without compactness. Very recently, Hsu, Wang and Zhao [13] were able to overcome this trouble by proving that the associated Poincaré map is asymptotically compact on any bounded set of the phase space to conclude that the system admits a global attractor, under the appropriate assumptions, through the abstract theory developed by Magal and Zhao [23]. The second handicap one should overcome is ascertaining the linearized stability of the trivial and semi-trivial steady states of the model. However the linearized system at all these states is cooperative, the "compactness" of the flow is as well needed for applying the classical Krein–Rutman theory in order to infer the existence of a principal eigenvalue whose sign can provide with the local attractive, or repulsive, character of these steady states. Also this difficulty has been recently overcome by Hsu, Wang and Zhao in [13,14] through a generalized Krein–Rutman Theorem going back to Nussbaum [25]. But, in order to apply the abstract theory of [25], the authors of [13,14] had to impose some slightly severe restrictions on a number of coefficients of the model.

The first goal of this paper is removing all these restrictions by adopting a direct approach to the problem from an elliptic perspective, rather than the parabolic one of Hsu, Wang and Zhao [13,14], which seems more sophisticated technically. Besides the principal eigenvalue of the linearized system is an important threshold predicting the persistence of the species in a single population model, it also predicts the coexistence for the two population model. Therefore, it is a categorical imperative to analyze the dependence, or sensitivity, of the principal eigenvalue with respect to the most significant parameters of the model from the ecological point of view. Here relies the second goal of this paper.

Although, very recently, Wang and Zhao, [29, Th. 2.3], found some sharp abstract results on the existence of principal eigenvalues for an elliptic eigenvalue problem associated with a linear parabolic cooperative system with some zero diffusion coefficients, in order to establish the simplicity and strict dominance of the principal eigenvalue of (4.28) we had to combine our (crucial) Lemmas 2.1, 2.2, and 2.3 with [29, Th. 2.3], which is far from being an easy task from a technical point of view. Incidentally, as for most of the results of this paper the algebraic simplicity and strict dominance of the principal eigenvalue do not seem to be really necessary, invoking to [29, Th. 2.3] to get out results might be unnecessary, though certainly [29, Th. 2.3] strengthens the findings of this paper.

This paper is distributed as follows. In Section 2, we study an eigenvalue problem which plays an essential role in river ecology. Basically, we establish the existence and the uniqueness of the principal eigenvalue of the eigenvalue problems associated with the system analyzed in [8]. Section 3 is devoted to the study of the qualitative dependence of this principal eigenvalue on the several parameters involved in the setting of the model. In Section 4, we incorporate the factor of vertical variation into the system of [8] to study a generalized system with light limitation. At the bright shared by our analysis, in Section 5 we will discuss the combined effects of diffusion, advection, depth and length of the river, exchanging rate between the main channel and the storage zones, as well as cross-sectional areas ratios, on the persistence of the single species.

2. A pivotal eigenvalue problem

In river ecology, the following linear parabolic problem of cooperative type plays a crucial role

$$\begin{cases} \frac{\partial Z}{\partial t} = \delta \frac{\partial^2 Z}{\partial x^2} - \nu \frac{\partial Z}{\partial x} + \alpha(Z_S - Z) + \beta_1(x) Z, & 0 < x < L,\ t > 0, \\ \frac{\partial Z_S}{\partial t} = -\alpha \frac{A}{A_S}(Z_S - Z) + \beta_2(x) Z_S, & \\ \nu Z(0,t) - \delta \frac{\partial Z}{\partial x}(0,t) = 0,\ \frac{\partial Z}{\partial x}(L,t) = 0, & t > 0, \\ Z(x,0) = Z^0(x) \geq 0,\ Z_S(x,0) = Z_S^0(x) \geq 0, & 0 < x < L, \end{cases} \tag{2.1}$$

where $\beta_1, \beta_2 \in \mathcal{C}[0, L]$ are given continuous functions, δ, α, ν, A, A_S and L are positive parameters, and Z^0, Z_S^0 stand for the initial conditions (the reader is sent to [8,14] for any further required detail). The set of pairs (ψ, φ) for which

$$Z(x,t) = e^{-\lambda t} \psi(x), \qquad Z_S(x,t) = e^{-\lambda t} \varphi(x),$$

solve (2.1) for some $\lambda \in \mathbb{R}$ satisfies the eigenvalue problem

$$\begin{cases} -\delta \psi'' + \nu \psi' - \beta_1(x) \psi + \alpha \psi - \alpha \varphi = \lambda \psi, & 0 < x < L, \\ -\alpha \frac{A}{A_S} \psi + (\alpha \frac{A}{A_S} - \beta_2(x)) \varphi = \lambda \varphi, & \\ \nu \psi(0) - \delta \psi'(0) = 0,\ \psi'(L) = 0. & \end{cases} \tag{2.2}$$

Consequently, studying the existence, the uniqueness and the sensitivity properties of the principal eigenvalue of (2.2) is imperative to analyze the dynamics of (2.1). By a principal eigenvalue it is meant a value of $\lambda \in \mathbb{R}$ for which the corresponding solution of (2.2) exists and it satisfies $\psi > 0$ and $\varphi > 0$ in $[0, L]$.

As the second equation of (2.2) yields

$$\varphi(x) = \frac{-\alpha \frac{A}{A_S}}{\lambda + \beta_2(x) - \alpha \frac{A}{A_S}} \psi(x) \qquad \forall\, x \in [0, L], \tag{2.3}$$

and $\alpha A/A_S > 0$, in order to guarantee that φ is well defined and that $\varphi \gg 0$, in the sense that $\varphi(x) > 0$ for all $x \in [0, L]$, throughout this paper we impose that

$$\lambda < \alpha \frac{A}{A_S} - \beta_2(x) \qquad \text{for all } x \in [0, L]. \tag{2.4}$$

Moreover, we also require

$$\alpha \frac{A}{A_S} - \beta_2(x) > 0 \qquad \text{for all } x \in [0, L] \tag{2.5}$$

and denote

$$\|\beta_2\|_\infty := \max_{x \in \bar{\Omega}} \beta_2(x), \qquad Q := A/A_S, \qquad \lambda_c := \alpha Q - \|\beta_2\|_\infty. \tag{2.6}$$

By the continuity of β_2, it follows from (2.4) and (2.5) that

$$\lambda < \lambda_c \quad \text{and} \quad \lambda_c := \alpha Q - \|\beta_2\|_\infty > 0. \tag{2.7}$$

Substituting (2.3) into the first equation of (2.2), it is apparent that, under condition (2.4), λ is a principal eigenvalue of (2.2) if, and only if, there exists $\psi > 0$ such that

$$\begin{cases} -\delta\psi'' + \nu\psi' - \beta_1\psi + \alpha\psi + \frac{\alpha^2 Q}{\lambda+\beta_2-\alpha Q}\psi = \lambda\psi & \text{in } (0, L), \\ \nu\psi(0) - \delta\psi'(0) = 0, \ \ \psi'(L) = 0. \end{cases} \tag{2.8}$$

In such case, thanks to [20, Th. 7.10], one has that $\psi \gg 0$, in the sense that

$$\psi(x) > 0 \quad \text{for all } x \in [0, L]. \tag{2.9}$$

Any of those functions ψ's, which are unique up to a multiplicative constant, is usually referred to as the *principal eigenfunction* associated with λ. The main result of this section establishes the existence and the uniqueness of the principal eigenvalue of this problem. It can be stated as follows. By a principal eigenvalue it is meant a value of λ associated with it there is a positive eigenfunction, $\psi > 0$.

Theorem 2.1. *Suppose $\lambda_c > 0$ and there are $r_0 > 0$, $M > 0$ and $x_* \in [0, L]$ such that $\beta_2(x_*) = \|\beta_2\|_\infty$ and*

$$|\beta_2(x) - \beta_2(x_*)| \le M|x - x_*| \qquad \textit{for all} \quad x \in [x_* - r_0, x_* + r_0] \cap [0, L]. \tag{2.10}$$

In other words, β_2 is locally Lipschitz at some point $x_* \in \beta_2^{-1}(\|\beta_2\|_\infty)$. Then, (2.2) possesses a unique principal eigenvalue $\lambda_p \in (-\infty, \lambda_c)$. Moreover,

$$\operatorname{sign} \lambda_p = \operatorname{sign} \lambda_\pi,$$

where λ_π stands for the (unique) principal eigenvalue of

$$\begin{cases} -\delta\psi'' + \nu\psi' - \beta_1\psi + \alpha\psi + \frac{\alpha^2 Q}{\beta_2 - \alpha Q}\psi = \lambda\psi \quad \text{in } (0, L), \\ \nu\psi(0) - \delta\psi'(0) = 0, \quad \psi'(L) = 0. \end{cases} \tag{2.11}$$

Furthermore, λ_p is algebraically simple and strictly dominant.

The rest of the section is devoted to the proof of Theorem 2.1. First, we will deliver two technical lemmas needed in the proof. Then, we will complete it.

2.1. Three auxiliary lemmas of technical nature

Lemma 2.1. *For any given $r > 0$, $\delta_1 > 0$, $\delta_2 > 0$ and $\epsilon > 0$, let $\sigma_1(\epsilon)$ denote the principal eigenvalue of*

$$\begin{cases} -\delta_1\phi''(x) - \dfrac{\delta_2}{\epsilon + |x|}\phi(x) = \sigma\phi(x), \quad x \in (-r, r), \\ \phi(-r) = \phi(r) = 0. \end{cases} \tag{2.12}$$

Then $\sigma_1(\epsilon) < -\delta_2/(2r)$ for sufficiently small $\epsilon > 0$.

Proof. By the monotonicity of the principal eigenvalue with respect to the potential (e.g., [19, Prop. 3.2], or [20, Prop. 8.3]), $\sigma_1(\epsilon)$ is increasing in ϵ. Moreover, $\sigma_1(\epsilon) < \delta_1[\pi/(2r)]^2$ for all $\epsilon > 0$. Assume, by contradiction, that there is a sequence $\epsilon_n \downarrow 0$ such that $\sigma_1(\epsilon_n) \downarrow \sigma_\omega \geq -\delta_2/(2r)$ as $n \to \infty$. Then,

$$-\frac{\delta_2}{2r} \leq \sigma_\omega \leq \sigma_1(\epsilon_n) \leq \delta_1\left(\frac{\pi}{2r}\right)^2, \qquad n \geq 1.$$

Subsequently, for each $n \geq 1$, we denote by $\phi_n \gg 0$ the principal eigenfunction associated with $\sigma_1(\epsilon_n)$ normalized so that $\int_{-r}^{r}(\phi_n')^2 = 1$. Then,

$$\begin{cases} -\delta_1\phi_n''(x) = \left(\dfrac{\delta_2}{\epsilon_n + |x|} + \sigma_1(\epsilon_n)\right)\phi_n(x), \quad x \in (-r, r), \\ \phi_n(-r) = \phi_n(r) = 0. \end{cases} \tag{2.13}$$

Multiplying the equation by ϕ_n and integrating by parts in $(-r, r)$, we find that

$$\int_{-r}^{r}\left(\frac{\delta_2}{\epsilon_n + |x|} + \sigma_1(\epsilon_n)\right)\phi_n^2(x)\,dx = \delta_1 \qquad \forall\, n \geq 1. \tag{2.14}$$

By the Sobolev imbeddings (see, e.g., [20, Cor. 4.1]), the sequence $\{\phi_n\}_{n\geq 1}$ is bounded in the space of Hölder continuous functions $\mathcal{C}^{0,1/2}[-r, r]$. Moreover, by the theorem of Rellich and Kondrachov (see, e.g., [20, Th. 4.5]), for every $\beta < 1/2$, the imbedding $H^1(-r, r) \hookrightarrow \mathcal{C}^{0,\beta}[-r, r]$

is compact and, hence, there exists $\phi_\omega \in \mathcal{C}^{0,1/4}[-r,r]$ such that, along some subsequence, relabeled by n, one has that

$$\lim_{n\to\infty} \|\phi_n - \phi_\omega\|_{\mathcal{C}^{0,1/4}[-r,r]} = 0. \tag{2.15}$$

In particular, $\phi_n \to \phi_\omega$ uniformly in $[-r,r]$ as $n \to \infty$.

On the other hand, as soon as $0 < \epsilon_n < r$, we have that

$$\frac{\delta_2}{\epsilon_n + |x|} + \sigma_1(\epsilon_n) > \frac{\delta_2}{2r} + \sigma_1(\epsilon_n) \geq \frac{\delta_2}{2r} + \sigma_\omega \geq 0, \qquad |x| \leq r, \tag{2.16}$$

and, consequently, thanks to (2.14), the functions

$$f_n := \left(\frac{\delta_2}{\epsilon_n + |\cdot|} + \sigma_1(\epsilon_n)\right)\phi_n^2, \qquad n \geq 1,$$

satisfy $f_n \in L^1(-r,r)$, $f_n \geq 0$ for sufficiently large n, and $\int_{-r}^r f_n = \delta_1$ for all $n \geq 1$. Thus, according to the Fatou lemma (see, e.g., [5, Lem. IV.1]),

$$f := \liminf_{n\to\infty} f_n = \left(\frac{\delta_2}{|\cdot|} + \sigma_\omega\right)\phi_\omega^2 \in L^1(-r,r) \tag{2.17}$$

and

$$0 \leq \int_{-r}^{r} \left(\frac{\delta_2}{|x|} + \sigma_\omega\right)\phi_\omega^2(x)\,dx \leq \delta_1. \tag{2.18}$$

Suppose $\phi_\omega(0) > 0$. Then, by continuity, there exists $\eta > 0$ such that $\phi_\omega(x) > \phi_\omega(0)/2$ for all $x \in [-\eta, \eta]$ and hence, since

$$\frac{\delta_2}{|x|} + \sigma_\omega \geq \frac{\delta_2}{r} + \sigma_\omega > \frac{\delta_2}{2r} + \sigma_\omega \geq 0,$$

we find that

$$\int_{-r}^{r} \left(\frac{\delta_2}{|x|} + \sigma_\omega\right)\phi_\omega^2(x)\,dx \geq (\phi_\omega(0)/2)^2 \left[\delta_2 \int_{-\eta}^{\eta} \frac{dx}{|x|} + 2\eta\sigma_\omega\right] = \infty,$$

which contradicts (2.18). Therefore,

$$\lim_{n\to\infty} \phi_n(0) = \phi_\omega(0) = 0. \tag{2.19}$$

On the other hand, according to (2.13) and (2.16), we find that $\phi_n''(x) < 0$ for all $x \in (-r,r)$ and, hence, $x \mapsto \phi_n'(x)$ is decreasing in $[-r,r]$. Also, by symmetry, $\phi_n'(-r) = -\phi_n'(r)$ and $\phi_n'(0) = 0$.

As, for every $\eta \in (0, r)$, the right hand side of Eq. (2.13) approximates $(\delta_2/|\cdot| + \sigma_\omega)\phi_\omega \in \mathcal{C}([-r, r] \setminus \{0\})$ uniformly in $[-r, -\eta] \cup [\eta, r]$, for each $\eta \in (0, r)$ there exists a constant $C_\eta > 0$ such that

$$|\phi_n''| \le C_\eta \qquad \text{in } [-r, -\eta] \cup [\eta, r] \qquad \forall\, n \ge 1.$$

Thus, combining the theorem of Ascoli and Arzela with a diagonal scheme, it becomes apparent that there exists $\psi_\omega \in \mathcal{C}([-r, r] \setminus \{0\})$, such that, along some subsequence, labeled again by n, we have that

$$\lim_{n\to\infty} \phi_n' = \psi_\omega \qquad \text{in } \mathcal{C}_{\text{loc}}([-r, r] \setminus \{0\}).$$

Necessarily, $\psi_\omega = \phi_\omega'$ in $[-r, r] \setminus \{0\}$ and, consequently, much like ϕ_n', $n \ge 1$, we find that $\phi_\omega' \ge 0$ in $[-r, 0)$ and $\phi_\omega' \le 0$ in $(0, r]$. Thus, (2.19) implies that $\phi_\omega = 0$ in $[-r, r]$ and, consequently, $\psi_\omega = \phi_\omega' = 0$ in $[-r, r] \setminus \{0\}$. Therefore,

$$\lim_{n\to\infty} \phi_n' = 0 \qquad \text{in } \mathcal{C}_{\text{loc}}([-r, r] \setminus \{0\}). \tag{2.20}$$

As we already know that, for every $x \in [-r, r]$, the following inequalities hold

$$\phi_n'(-r) \ge \phi_n'(x) \ge \phi_n'(r),$$

(2.20) implies that

$$0 \le \int_{-r}^{r} (\phi_n')^2 \le 2r(\phi_n'(r))^2 \mapsto 0 \qquad \text{as} \quad n \to \infty,$$

which contradicts $\int_{-r}^{r} (\phi_n')^2 = 1$ and ends the proof. □

Lemma 2.2. *For any given $r > 0$, $\delta_1 > 0$, $\delta_2 > 0$, $\epsilon > 0$ and $\kappa \ne 0$, let $\sigma_1(\epsilon)$ denote the principal eigenvalue of*

$$\begin{cases} -\delta_1 \phi''(x) - \dfrac{\delta_2}{\epsilon + |x|}\phi(x) = \sigma\phi(x), & x \in (-r, 0), \\ \phi(-r) = 0, \quad \phi'(0) + \kappa\phi(0) = 0. \end{cases} \tag{2.21}$$

Then, $\sigma_1(\epsilon) < -\delta_2/(2r)$ for sufficiently small $\epsilon > 0$.

Proof. We will adapt the proof of Lemma 2.1. By [2, Prop. 3.3] (or [20, Prop. 8.3]), the map $\epsilon \mapsto \sigma_1(\epsilon)$, $\epsilon > 0$, is increasing. Assume, by contradiction, that

$$\sigma_\omega := \lim_{\epsilon \downarrow 0} \sigma_1(\epsilon) \ge -\frac{\delta_2}{2r}.$$

Then,

$$-\frac{\delta_2}{2r} \le \sigma_\omega \le \sigma_1(\epsilon) \qquad \text{for all } \epsilon > 0.$$

Let $\phi_\epsilon \gg 0$ be the principal eigenfunction associated with $\sigma_1(\epsilon)$ normalized so that

$$\|\phi_\epsilon\|_{H^1(-r,0)} = 1, \qquad \epsilon > 0. \tag{2.22}$$

Obviously, as soon as $\epsilon \in (0, r)$, we have that

$$-\delta_1 \phi_\epsilon''(x) = \left(\frac{\delta_2}{\epsilon + |x|} + \sigma_1(\epsilon)\right)\phi_\epsilon(x) > 0 \qquad \forall\, x \in (-r, 0)$$

and, hence, ϕ_ϵ' is decreasing in $[-r, 0]$ for all $\epsilon \in (0, r)$. As in the proof of Lemma 2.1, by the Sobolev embeddings, there is a constant $C > 0$ such that $\|\phi_\epsilon\|_{C^{1/2}[-r,0]} \le C$ for all $\epsilon > 0$. Therefore, by compactness, there exist $\phi_\omega \in C^{1/4}[-r, 0]$ and a subsequence $0 < \epsilon_n < r$, $n \ge 1$, such that $\epsilon_n \to 0$ and $\phi_n := \phi_{\epsilon_n} \to \phi_\omega$ in $C^{1/4}[-r, 0]$ as $n \to \infty$. By adapting the proof of Lemma 2.1, it is apparent that $\phi_\omega \in \mathcal{C}^2[-r, 0)$ and that, along some subsequence, relabeled by n, we have that

$$\lim_{n\to\infty} \phi_n = \phi_\omega \qquad \text{in} \quad \mathcal{C}^2_{\text{loc}}[-r, 0) \cap C^{1/4}[-r, 0]. \tag{2.23}$$

As

$$-\delta_1 \phi_\omega''(x) = \left(\frac{\delta_2}{|x|} + \sigma_\omega\right)\phi_\omega(x) \qquad \forall\, x \in (-r, 0) \tag{2.24}$$

and $\phi_\omega \ge 0$, either $\phi_\omega = 0$, or $\phi_\omega(x) > 0$ for all $x \in (-r, 0)$. Indeed, if there exists $x_0 \in (-r, 0)$ such that $\phi_\omega(x_0) = 0$, necessarily $\phi_\omega'(x_0) = 0$ and, by the existence and the uniqueness of solution for the associated Cauchy problem, we can infer that $\phi_\omega = 0$ in $[-r, 0]$. Therefore, $\phi_\omega(x) > 0$ for all $x \in (-r, 0)$ if $\phi_\omega \ne 0$. Moreover, in such case, since

$$\phi_\omega(-r) = \lim_{n\to\infty} \phi_n(-r) = 0,$$

we also have that $\phi_\omega'(-r) > 0$.

Suppose $\phi_\omega = 0$. Then, $\phi_\omega' = 0$ and, since

$$\phi_n'(-r) \ge \phi_n'(x) \ge \phi_n'(0) = -\kappa \phi_n(0)$$

for all $n \ge 1$ and $-r < x < 0$, it follows from (2.23) that $\phi_n' \to 0$ uniformly in $[-r, 0]$ and, hence, $\phi_n \to 0$ in $C^1[-r, 0]$ as $n \to \infty$, which contradicts (2.22). Consequently, $\phi_\omega(x) > 0$ for all $x \in (-r, 0)$.

Suppose $\phi_\omega(0) = 0$. Then, as $\phi_n'' < 0$ in $(-r, 0)$, for any $-r < x < y < 0$, we have that

$$\phi_n'(-r) \ge \phi_n'(x) \ge \phi_n'(y) \ge \phi_n'(0) = -\kappa \phi_n(0)$$

and letting $n \to \infty$ yields

$$\phi'_\omega(-r) \geq \phi'_\omega(x) \geq \phi'_\omega(y) \geq 0.$$

Thus,

$$\phi'_\omega(0) := \lim_{x \downarrow 0} \phi'_\omega(x) \geq 0$$

is well defined, which entails $\phi_\omega \in \mathcal{C}^1[-r, 0]$. If $\phi'_\omega(0) = 0$, then (2.24) implies $\phi_\omega = 0$, which is impossible. Therefore, $\phi'_\omega(0) > 0$ and substituting the asymptotic expansion

$$\phi_\omega(x) = \phi'_\omega(0)x + o(x) \qquad \text{as } x \uparrow 0,$$

in (2.24), we find that

$$-\delta_1 \phi''_\omega(x) = -\delta_2 \phi'_\omega(0) + o(1) \qquad \text{as } x \uparrow 0,$$

which entails $\phi''_\omega(x) > 0$ for sufficiently small $x > 0$; also impossible. This shows that, necessarily, $\phi_\omega(0) > 0$. By continuity, there is $\eta \in (0, r)$ such that

$$\phi_\omega(x) \geq \phi_\omega(0)/2 \qquad \forall\, x \in [-\eta, 0]. \tag{2.25}$$

On the other hand, multiplying the ϕ_n-equation by ϕ_n and integrating in $[-r, 0]$, we find that

$$\delta_1 \kappa \phi_n^2(0) + \delta_1 \int_{-r}^{0} (\phi'_n)^2 = \int_{-r}^{0} \left(\frac{\delta_2}{\epsilon_n + |x|} + \sigma_1(\epsilon_n) \right) \phi_n^2(x)dx. \tag{2.26}$$

Thus, according to (2.22) and letting $n \to \infty$ in (2.26), we find from the Fatou lemma that

$$0 \leq \int_{-r}^{0} \left(\frac{\delta_2}{|x|} + \sigma_\omega \right) \phi_\omega^2(x)dx \leq \delta_1 \kappa \phi_\omega^2(0) + \delta_1.$$

However,

$$\int_{-r}^{0} \left(\frac{\delta_2}{|x|} + \sigma_\omega \right) \phi_\omega^2(x)dx \geq \int_{-\eta}^{0} \left(\frac{\delta_2}{|x|} - \frac{\delta_2}{2r} \right) \frac{1}{4} \phi_\omega^2(0)dx = \infty,$$

which is a contradiction. The proof is complete. □

Naturally, by performing the change of variable $y := -x$, Lemma 2.2 also provides us with the next result:

Lemma 2.3. *For any given $r > 0$, $\delta_1 > 0$, $\delta_2 > 0$, $\epsilon > 0$ and $\kappa \neq 0$, let $\sigma_1(\epsilon)$ denote the principal eigenvalue of*

$$\begin{cases} -\delta_1 \phi''(x) - \dfrac{\delta_2}{\epsilon + |x|} \phi(x) = \sigma \phi(x), & x \in (0, r), \\ \phi'(0) - \kappa \phi(0) = 0, \qquad \phi(r) = 0. \end{cases} \tag{2.27}$$

Then, $\sigma_1(\epsilon) < -\delta_2/(2r)$ for sufficiently small $\epsilon > 0$.

2.2. Proof of Theorem 2.1

Throughout this paper, given $a, b, p_a, p_b, q_a, q_b \in \mathbb{R}$ with $a < b$, a linear second order uniformly elliptic operator $\mathfrak{L}$ in $[a, b]$ and the boundary operator $\mathfrak{B} : \mathcal{C}[a, b] \to \mathbb{R}^2$ defined by

$$\mathfrak{B}\xi := \begin{cases} p_a\, \xi(a) + q_a\, \xi'(a), \\ p_b\, \xi(b) + q_b\, \xi'(b), \end{cases} \qquad \xi \in \mathcal{C}[a, b],$$

we denote by $\sigma_1[\mathfrak{L}, \mathfrak{B}, (a, b)]$ the principal eigenvalue of

$$\begin{cases} \mathfrak{L}\psi = \sigma \psi, & \text{in } (a, b), \\ \mathcal{B}\psi = 0, & \text{on } \{a, b\} = \partial(a, b). \end{cases}$$

When $p_a = p_b = 1$ and $q_a = q_b = 0$, we simply denote $\mathfrak{D} := \mathfrak{B}$ (Dirichlet boundary conditions). Similarly, if $p_a = p_b = 0$ and $q_a = q_b = 1$, we denote $\mathfrak{N} := \mathfrak{B}$ (Neumann boundary conditions). Making the special choices

$$a = 0, \quad b = L, \qquad \mathfrak{B}\xi := \begin{cases} \nu \xi(0) - \delta \xi'(0), \\ \xi'(L), \end{cases} \qquad \xi \in \mathcal{C}[0, L], \tag{2.28}$$

$$\mathfrak{L} := -\delta D^2 + \nu D - \beta_1, \qquad D := d/dx, \tag{2.29}$$

and introducing the function $F : (-\infty, \lambda_c) \to \mathbb{R}$ defined by

$$F(\lambda) := \sigma_1 \left[\mathfrak{L} + \alpha + \frac{\alpha^2 Q}{\lambda + \beta_2(x) - \alpha Q}, \mathfrak{B}, (0, L) \right], \tag{2.30}$$

to complete the proof of Theorem 2.1, we should show the existence of a unique $\lambda_p \in (-\infty, \lambda_c)$ such that

$$F(\lambda_p) = \lambda_p. \tag{2.31}$$

As $\lambda_\pi = F(0)$, the second assertion of the theorem establishes that

$$\operatorname{sign} \lambda_p = \operatorname{sign} F(0).$$

Thanks to the monotonicity of the principal eigenvalue with respect to the potential (see, e.g., [20, Prop. 8.3]), the map $\lambda \mapsto F(\lambda)$ is decreasing. Moreover, the change of variable

$$\phi(x) := e^{-\frac{\nu}{2\delta}x}\psi(x), \qquad x \in [0, L],$$

transforms (2.8) into the equivalent eigenvalue problem

$$\begin{cases} -\delta\phi'' + \frac{\nu^2}{4\delta}\phi - \beta_1(x)\phi + \alpha\phi + \frac{\alpha^2 Q}{\lambda+\beta_2(x)-\alpha Q}\phi = \lambda\phi, & 0 < x < L, \\ \nu\phi(0) - 2\delta\phi'(0) = 0, \quad \nu\phi(L) + 2\delta\phi'(L) = 0, \end{cases} \tag{2.32}$$

where the drift term of the differential operator has been removed. Thus, setting

$$\mathfrak{L}_t := -\delta D^2 + \frac{\nu^2}{4\delta} - \beta_1, \qquad \mathfrak{B}_t\xi := \begin{cases} \nu\xi(0) - 2\delta\xi'(0), \\ \nu\xi(L) + 2\delta\xi'(L), \end{cases} \qquad \xi \in \mathcal{C}[0, L],$$

by the uniqueness of the principal eigenvalue (see, e.g., [20, Th. 7.7]), it becomes apparent that

$$F(\lambda) = \sigma_1\left[\mathfrak{L}_t + \alpha + \frac{\alpha^2 Q}{\lambda + \beta_2(x) - \alpha Q}, \mathfrak{B}_t, (0, L)\right]$$

for all $\lambda < \lambda_c$. To carry out the technical details of the proof of the theorem, we will distinguish three different cases, according to the nature of $\beta_2(x)$.

Case I: There are $0 \le a < b \le L$ **such that** $\beta_2(x) = \|\beta_2\|_\infty$ **for all** $x \in [a, b]$**.** By the continuous dependence of the principal eigenvalue with respect to the potential (see, e.g., Cano-Casanova and López-Gómez [2, Cor. 3.4], or [20, Cor. 8.1]), it follows that

$$\lim_{\lambda\downarrow-\infty} F(\lambda) = \sigma_1[\mathfrak{L}_t, \mathfrak{B}_t, (0, L)] + \alpha. \tag{2.33}$$

Moreover, according to Proposition 8.1, Corollary 8.2 and Proposition 8.3 of [20], it becomes apparent that

$$\begin{aligned} F(\lambda) &= \sigma_1\left[\mathfrak{L}_t + \alpha + \alpha^2 Q/(\lambda + \beta_2(x) - \alpha Q), \mathfrak{B}_t, (0, L)\right] \\ &\le \sigma_1\left[\mathfrak{L}_t + \alpha + \alpha^2 Q/(\lambda + \beta_2(x) - \alpha Q), \mathfrak{D}, (0, L)\right] \\ &\le \sigma_1\left[\mathfrak{L}_t + \alpha + \alpha^2 Q/(\lambda + \beta_2(x) - \alpha Q), \mathfrak{D}, (a, b)\right] \\ &= \sigma_1\left[\mathfrak{L}_t + \alpha + \alpha^2 Q/(\lambda + \|\beta\|_\infty - \alpha Q), \mathfrak{D}, (a, b)\right]. \end{aligned}$$

Thus, we find from (2.7) that

$$F(\lambda) \le \sigma_1\left[\mathfrak{L}_t + \alpha + \frac{\alpha^2 Q}{\lambda - \lambda_c}, \mathfrak{D}, (a, b)\right] \qquad \text{for all } \lambda < \lambda_c$$

and therefore

$$\lim_{\lambda\uparrow\lambda_c} F(\lambda) = -\infty. \tag{2.34}$$

Consequently, as the map $\lambda \mapsto F(\lambda)$ is decreasing, there is a unique λ, denoted by λ_p, such that $F(\lambda_p) = \lambda_p$. Moreover, as $\lambda_c > 0$, it becomes apparent that $\lambda_p > 0$ if $F(0) > 0$, whereas $\lambda_p < 0$ if $F(0) < 0$ and $\lambda_p = 0$ if $F(0) = 0$, which ends the proof of (2.31) in this case.

Case II: $x_* \in (0, L)$**.** According to (2.10), we can take $0 < r_0 < \min\{x_*, L - x_*\}$ such that

$$\beta_2(x) - \beta_2(x_*) = \beta_2(x) - \|\beta_2\|_\infty \geq -M|x - x^*|, \qquad x \in (x_* - r_0, x_* + r_0).$$

Thus, denoting $J_r := (x_* - r, x_* + r)$, by the properties of the principal eigenvalue, we obtain that, for every $r \in (0, r_0)$ and $\lambda < \lambda_c$,

$$\begin{aligned} F(\lambda) &= \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q / (\lambda + \beta_2(x) - \alpha Q), \mathfrak{B}_t, (0, L) \right] \\ &\leq \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q / (\lambda + \beta_2(x) - \alpha Q), \mathfrak{D}, (0, L) \right] \\ &\leq \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q / (\lambda + \beta_2(x) - \alpha Q), \mathfrak{D}, J_r \right] \\ &\leq \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q / (\lambda + \|\beta_2\|_\infty - M|x - x_*| - \alpha Q), \mathfrak{D}, J_r \right] \\ &= \sigma_1 \left[\mathfrak{L}_t + \alpha - \alpha^2 Q / (\lambda_c - \lambda + M|x - x_*|), \mathfrak{D}, J_r \right]. \end{aligned}$$

Thus, making the change of variable $y := x - x_*$, Lemma 2.1 implies that

$$\begin{aligned} F(\lambda) &\leq \frac{\nu^2}{4\delta} + \|\beta_1\|_\infty + \alpha + \sigma_1 \left[-\delta D^2 - \frac{\alpha^2 Q}{\lambda_c - \lambda + M|y|}, \mathfrak{D}, (-r, r) \right] \\ &< \frac{\nu^2}{4\delta} + \|\beta_1\|_\infty + \alpha - \frac{\alpha^2 Q}{2Mr} \end{aligned}$$

for all $r \in (0, r_0)$ and $\lambda < \lambda_c$ sufficiently close to λ_c. Therefore, as this estimate is valid for arbitrarily small $r > 0$, (2.34) also holds in this case and the proof of (2.31) is complete if $x_* \in (0, L)$.

Case III: $x_* \in \{0, L\}$**.** Suppose $x_* = L$, let $r_0 \in (0, L)$ and $M > 0$ be such that

$$\beta_2(x) - \beta_2(L) = \beta_2(x) - \|\beta_2\|_\infty \geq M(x - L) \qquad \text{for all} \quad x \in [L - r_0, L],$$

and consider, for every $0 < r < r_0$,

$$J_r := (L - r, L), \qquad \mathfrak{B}_0 \xi := \begin{cases} \xi(L - r), \\ \nu \xi(L) + 2\delta \xi'(L), \end{cases} \qquad \xi \in \mathcal{C}[L - r, L].$$

Then, according to [20, Pr. 8.2],

$$\begin{aligned} F(\lambda) &= \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q / (\lambda + \beta_2(x) - \alpha Q), \mathfrak{B}_t, (0, L) \right] \\ &\leq \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q / (\lambda + \beta_2(x) - \alpha Q), \mathfrak{B}_0, (L - r, L) \right] \end{aligned}$$

$$\le \sigma_1 \left[\mathfrak{L}_t + \alpha + \alpha^2 Q/\left(\lambda + \|\beta_2\|_\infty - M|x-L| - \alpha Q\right), \mathfrak{B}_0, (L-r, L) \right]$$
$$= \sigma_1 \left[\mathfrak{L}_t + \alpha - \alpha^2 Q/\left(\lambda_c - \lambda + M|x-L|\right), \mathfrak{B}_0, (L-r, L) \right].$$

Thus, by performing the change of variable $y := x - L$, we find from the monotonicity of the principal eigenvalue with respect to the potential that

$$F(\lambda) \le \frac{\nu^2}{4\delta} + \|\beta_1\|_\infty + \alpha + \sigma_1 \left[-\delta D^2 - \frac{\alpha^2 Q}{\lambda_c - \lambda + M|y|}, \tilde{\mathfrak{B}}_0, (-r, 0) \right],$$

where

$$\tilde{\mathfrak{B}}_0 \xi := \begin{cases} \xi(-r), \\ \nu\xi(0) + 2\delta\xi'(0), \end{cases} \qquad \xi \in \mathcal{C}[-r, 0].$$

Therefore, owing to Lemma 2.2, we conclude that

$$F(\lambda) \le \frac{\nu^2}{4\delta} + \|\beta_1\|_\infty + \alpha - \frac{\alpha^2 A}{2A_S M r}$$

for sufficiently small $r \in (0, r_0)$ and $\lambda_c - \lambda$. Consequently, (2.34) holds true and the proof of (2.31) is also concluded in this case.

When $x_* = 0$, the previous argument can be easily adapted to complete the proof of (2.31) by using Lemma 2.3, instead of Lemma 2.2.

Lastly, we will use [29, Th. 2.3] to complete the proof of the theorem. To this end, we consider the next one-parameter family of linear operators on $C[0, L]$

$$\mathbb{L}_\Lambda := \delta \frac{\partial^2}{\partial x^2} - \nu \frac{\partial}{\partial x} + (\beta_1(x) - \alpha) + \frac{\frac{\alpha^2 A}{A_S}}{\Lambda - (\beta_2(x) - \alpha \frac{A}{A_S})}$$

defined for

$$\Lambda > \|\beta_2\|_\infty - \alpha \frac{A}{A_S}.$$

By choosing $\Lambda_p := -\lambda_p$, from (2.31) it becomes apparent that there exists $\psi_p > 0$ such that

$$\mathbb{L}_{\Lambda_p} \psi_p = \Lambda_p \psi_p \ge \Lambda_p \psi_p.$$

Therefore, applying [29, Th. 2.3(i)] ends the proof of Theorem 2.1.

Remark 2.1. It is worth pointing out that one can also use our Lemmas 2.1, 2.2, and 2.3, as well as some of the ideas of the proof of [29, Le. 4.1] to construct another suitable Λ_0 and $\psi_0 \ge 0, \not\equiv 0$ such that

$$\mathbb{L}_{\Lambda_0} \psi_0 \ge \Lambda_0 \psi_0.$$

Also in this case, [29, Theorem 2.3] ends the proof of Theorem 2.1.

Remark 2.2. Although the most pioneering ideas for establishing the existence and the uniqueness of the principal eigenvalue in the context of linear elliptic cooperative systems through the existence of a positive supersolution, ψ_0, seem to go back to [21, Th. 2.1(C1)], which was published 21 years ago, one should recognize that their adaptation to cover the more general setting of [29] is far from being an easy task, besides extremely useful.

3. Dependence of λ_p on the parameters

Throughout this section we always assume that (2.5) holds and work under the general assumptions of Theorem 2.1. Consequently, the eigenvalue problem (2.2), or, equivalently, (2.8), possesses a unique principal eigenvalue λ_p. Naturally, λ_p depends on the several parameters and functions involved in the setting of these eigenvalue problems. Namely, ν, α, $\beta_1(x)$, $\beta_2(x)$, Q, δ and L. The main goal of this section is analyzing how varies λ_p as some of these parameters change. By construction, λ_p is the unique value of

$$\lambda < \lambda_c := \alpha Q - \|\beta_2\|_\infty$$

for which the eigenvalue problem

$$\begin{cases} -\delta\psi'' + \nu\psi' + (\alpha - \beta_1)\psi + \dfrac{\alpha^2 Q}{\lambda - \lambda_c + \beta_2(x) - \|\beta_2\|_\infty}\psi = \lambda\psi, \\ \delta\psi'(0) - \nu\psi(0) = 0, \quad \psi'(L) = 0, \end{cases} \tag{3.1}$$

admits a positive eigenfunction $\psi > 0$. By (2.7), $\lambda_c > 0$.

As the change of variable $\phi(x) := e^{-\frac{\nu}{2\delta}x}\psi(x)$, $x \in [0, L]$, transforms (3.1) into the equivalent eigenvalue problem (2.32), it is very appropriate to introduce the following *potential*

$$V := V(\lambda, \alpha, \beta_1, \beta_2, Q) = \beta_1 + \lambda - \frac{\alpha(\lambda + \beta_2)}{\lambda + \beta_2 - \alpha Q}. \tag{3.2}$$

In terms of V, the problem (2.32) can be expressed as

$$\begin{cases} -\delta\phi'' + \dfrac{\nu^2}{4\delta}\phi = V(\lambda, \alpha, \beta_1, \beta_2, Q)\phi, \\ 2\delta\phi'(0) - \nu\phi(0) = 0, \quad 2\delta\phi'(L) + \nu\phi(L) = 0. \end{cases} \tag{3.3}$$

As V is strictly increasing in λ, α, β_1 and β_2, and strictly decreasing in Q, the next monotonicity result for the principal eigenvalue $\lambda_p = \lambda_p(\nu, \alpha, \beta_1, \beta_2, Q)$ holds.

Theorem 3.1. *Suppose*

$$\hat{\nu} \geq \nu \geq 0, \qquad \hat{Q} \geq Q, \qquad \hat{\alpha} \leq \alpha, \qquad \hat{\beta}_1 \leq \beta_1, \qquad \hat{\beta}_2 \leq \beta_2. \tag{3.4}$$

Then,

$$\hat{\lambda}_p := \lambda_p(\hat{\nu}, \hat{\alpha}, \hat{\beta}_1, \hat{\beta}_2, \hat{Q}) \geq \lambda_p := \lambda_p(\nu, \alpha, \beta_1, \beta_2, Q).$$

Moreover, $\hat{\lambda}_p > \lambda_p$ if some of the inequalities of (3.4) is strict.

Proof. Suppose, on the contrary, that $\hat{\lambda}_p < \lambda_p$. Then, setting

$$W := V(\lambda_p, \alpha, \beta_1, \beta_2, Q), \qquad \hat{W} := V(\hat{\lambda}_p, \hat{\alpha}, \hat{\beta}_1, \hat{\beta}_2, \hat{Q}),$$

we find from the monotonicity properties of V that $\hat{W} < W$. Moreover, if we denote by $\phi > 0$ and $\hat{\phi} > 0$ the principal eigenfunctions associated with λ_p and $\hat{\lambda}_p$, normalized so that $\|\phi\|_\infty = \|\hat{\phi}\|_\infty$, then

$$\begin{cases} -\delta\phi'' + \dfrac{\nu^2}{4\delta}\phi = W\phi, \\ 2\delta\phi'(0) - \nu\phi(0) = 0, \ \ 2\delta\phi'(L) + \nu\phi(L) = 0, \end{cases} \tag{3.5}$$

and

$$\begin{cases} -\delta\hat{\phi}'' + \dfrac{\hat{\nu}^2}{4\delta}\hat{\phi} = \hat{W}\hat{\phi}, \\ 2\delta\hat{\phi}'(0) - \hat{\nu}\hat{\phi}(0) = 0, \ \ 2\delta\hat{\phi}'(L) + \hat{\nu}\hat{\phi}(L) = 0. \end{cases} \tag{3.6}$$

Hence, multiplying the ϕ-equation by $\hat{\phi}$, the $\hat{\phi}$-equation by ϕ, subtracting the resulting identities and integrating in $(0, L)$, yields

$$\begin{aligned} \int_0^L (W - \hat{W})\phi\hat{\phi} &= \frac{\nu^2 - \hat{\nu}^2}{4\delta} \int_0^L \phi\hat{\phi} + \delta\left[\phi\hat{\phi}' - \phi'\hat{\phi}\right]_{x=0}^{x=L} \\ &= \frac{\nu^2 - \hat{\nu}^2}{4\delta} \int_0^L \phi\hat{\phi} + \frac{\nu - \hat{\nu}}{2}\left[\phi(L)\hat{\phi}(L) + \phi(0)\hat{\phi}(0)\right]. \end{aligned}$$

As $\hat{W} < W$, $\phi \gg 0$ and $\hat{\phi} \gg 0$, the left hand side is positive and, hence,

$$\frac{\nu^2 - \hat{\nu}^2}{4\delta} \int_0^L \phi\hat{\phi} + \frac{\nu - \hat{\nu}}{2}\left[\phi(L)\hat{\phi}(L) + \phi(0)\hat{\phi}(0)\right] > 0. \tag{3.7}$$

On the other hand, we have that $\int_0^L \phi\hat{\phi} > 0$, $\phi(L) > 0$, $\hat{\phi}(L) > 0$, $\phi(0) > 0$ and $\hat{\phi}(0) > 0$. Indeed, if $\phi(L) = 0$, it follows from (3.5) that $\phi'(L) = 0$ and, hence, by the uniqueness of solution for the associated Cauchy problem, $\phi = 0$ in $[0, L]$. Similarly, $\phi = 0$ (resp. $\hat{\phi} = 0$) if $\phi(0) = 0$ (resp. $\hat{\phi}(0) = 0$, or $\hat{\phi}(L) = 0$). Therefore, we find from (3.7) that $\nu > \hat{\nu}$, which contradicts the choice $\hat{\nu} \geq \nu$. Consequently, $\lambda_p \leq \hat{\lambda}_p$.

Now, suppose that some of the inequalities of (3.4) is strict, but $\hat{\lambda}_p = \lambda_p$. Precisely, suppose some of the last four inequalities of (3.4) is strict. Then, $\hat{W} < W$ and, hence, (3.7) holds. Thus, $\nu > \hat{\nu}$, which contradicts the first requirement of (3.4). Consequently, $\hat{Q} = Q$, $\hat{\alpha} = \alpha$, $\hat{\beta}_1 = \beta_1$ and $\hat{\beta}_2 = \beta_2$. Therefore, $W = \hat{W}$ and, hence,

$$\frac{\nu^2-\hat{\nu}^2}{4\delta}\int_0^L \phi\hat{\phi} + \frac{\nu-\hat{\nu}}{2}\left[\phi(L)\hat{\phi}(L)+\phi(0)\hat{\phi}(0)\right]=0,$$

which implies $\nu=\hat{\nu}$. This ends the proof. □

As a consequence from Theorem 3.1, the next two results hold. In the first one, λ_p is regarded as a function of the parameter $Q = A/A_S$.

Theorem 3.2. *The map $Q \mapsto \lambda_p(Q)$ is increasing and*

$$\lim_{Q\uparrow\infty} \lambda_p(Q) = \sigma_1[\mathfrak{L}, \mathfrak{B}, (0, L)], \tag{3.8}$$

where $\mathfrak{L}$ and $\mathfrak{B}$ are given by (2.29) and (2.28), respectively.

Proof. According to Theorem 3.1, $\lambda_p(Q)$ is increasing. Moreover, due to (2.33), we have that

$$\lambda_p(Q) = F(\lambda_p(Q)) \le \sigma_1[\mathfrak{L}_t, \mathfrak{B}_t, (0, L)] + \alpha.$$

Hence,

$$\lambda_p(\infty) := \lim_{Q\uparrow\infty} \lambda_p(Q) \in \mathbb{R}$$

is well defined. In addition, by definition, we have that

$$\lambda_p(Q) = F(\lambda_p(Q)) = \sigma_1\left[\mathfrak{L} + \alpha + \frac{\alpha^2 Q}{\lambda_p(Q)+\beta_2-\alpha Q}, \mathfrak{B}, (0, L)\right]$$

for all $Q > 0$. By letting $Q \to \infty$ in this identity, (3.8) holds, by the continuous dependence of $\sigma_1[\mathfrak{L} + P, \mathfrak{B}, (0, L)]$ with respect to P (see [20, Cor. 8.1]). □

In the next result, the principal eigenvalue λ_p is regarded as a function of the parameter α, and it will be denoted by $\lambda_p(\alpha)$.

Theorem 3.3. *The map $\alpha \mapsto \lambda_p(\alpha)$ is decreasing and satisfies*

$$\lim_{\alpha\downarrow 0} \lambda_p(\alpha) = \sigma[\mathfrak{L}, \mathfrak{B}, (0, L)]. \tag{3.9}$$

$$\lim_{\alpha\uparrow\infty} \lambda_p(\alpha) = \frac{Q}{Q+1}\sigma_1\left[\mathfrak{L} - \beta_2/Q, \mathfrak{B}, (0, L)\right], \tag{3.10}$$

where $\mathfrak{L}$ and $\mathfrak{B}$ are given by (2.29) and (2.28), respectively.

Proof. The identity (3.9) is obvious. According to Theorem 3.1, $\alpha \mapsto \lambda_p(\alpha)$ is decreasing. Thus,

$$\lambda_p^* := \lim_{\alpha\uparrow\infty} \lambda_p(\alpha) \in [-\infty, \infty)$$

is well defined. Suppose $\lambda_p^* \in \mathbb{R}$. Then, letting $\alpha \uparrow \infty$ in the next identity

$$\lambda_p(\alpha) = \sigma_1 \left[\mathfrak{L} + \frac{\alpha(\lambda_p(\alpha) + \beta_2)}{\lambda_p(\alpha) + \beta_2 - \alpha Q}, \mathfrak{B}, (0, L) \right], \qquad \alpha > 0, \tag{3.11}$$

we find from [20, Cor. 8.1] that

$$\lambda_p^* = \sigma_1 \left[\mathfrak{L} - (\lambda_p^* + \beta_2)/Q, \mathfrak{B}, (0, L) \right] = \sigma_1 \left[\mathfrak{L} - \beta_2/Q, \mathfrak{B}, (0, L) \right] - \lambda_p^*/Q,$$

which implies

$$\lambda_p^* = \frac{Q}{Q+1} \sigma_1 \left[\mathfrak{L} - \beta_2/Q, \mathfrak{B}, (0, L) \right], \tag{3.12}$$

and ends the proof of (3.10). As getting the appropriate lower estimates for $\lambda_p(\alpha)$ as $\alpha \uparrow \infty$ seems rather involved, we will prove the result by combining the uniqueness of $\lambda_p(\alpha)$ with the implicit function theorem. Note that, setting

$$\mu_p(\epsilon) = \lambda_p(\alpha), \qquad \epsilon = 1/\alpha, \qquad \epsilon > 0,$$

the identity (3.11) can be equivalently expressed as

$$\mu_p(\epsilon) = \sigma_1 \left[\mathfrak{L} + \frac{\mu_p(\epsilon) + \beta_2}{\epsilon[\mu_p(\epsilon) + \beta_2] - Q}, \mathfrak{B}, (0, L) \right], \qquad \epsilon > 0. \tag{3.13}$$

Thus, it is natural to introduce the map

$$G(\mu, \epsilon) := \sigma_1 \left[\mathfrak{L} + \frac{\mu + \beta_2}{\epsilon(\mu + \beta_2) - Q}, \mathfrak{B}, (0, L) \right] - \mu, \qquad \epsilon(\mu + \|\beta_2\|_\infty) < Q.$$

According to Theorem 2.6 on page 377 of Kato [15], $(\mathfrak{L} + \frac{\mu+\beta_2}{\epsilon(\mu+\beta_2)-Q}, \mathfrak{B}, (0, L))$ is a holomorphic family of type (A) in μ and ϵ, within the region $\epsilon(\mu + \|\beta_2\|_\infty) < Q$. Therefore, due to Remark 2.9 on page 379 of [15], all the eigenvalues of $(\mathfrak{L} + \frac{\mu+\beta_2}{\epsilon(\mu+\beta_2)-Q}, \mathfrak{B}, (0, L))$ vary analytically with respect to μ and ϵ, as all of them are algebraically simple. Moreover,

$$G(\lambda_p^*, 0) = \sigma_1 \left[\mathfrak{L} - (\lambda_p^* + \beta_2)/Q, \mathfrak{B}, (0, L) \right] - \lambda_p^* = 0.$$

Suppose $\partial_\mu G(\lambda_p^*, 0) \neq 0$. Then, thanks to the implicit function theorem, there exist $\epsilon_0 > 0$ and a (unique) analytic map $\mu : (-\epsilon_0, \epsilon_0) \to \mathbb{R}$ such that

$$\mu(0) = \lambda_p^*, \qquad G(\mu(\epsilon), \epsilon) = 0 \qquad \text{for all } \epsilon \in (-\epsilon_0, \epsilon_0),$$

and $\mu = \mu(\epsilon)$ if $G(\mu, \epsilon) = 0$ with $(\mu, \epsilon) \sim (\lambda_p^*, 0)$. By the uniqueness of $\lambda_p(\alpha)$, necessarily $\mu(\epsilon) = \lambda_p(\alpha)$, $\epsilon = 1/\alpha$, for sufficiently large α. This would end the proof of the theorem, because $\mu(0) = \lambda_p^*$. Consequently, to complete the proof it suffices to show that $\partial_\mu G(\lambda_p^*, 0) \neq 0$.

Let $\varphi(\mu, \epsilon) \gg 0$ denote the principal eigenfunction associated with $G(\mu, \epsilon) + \mu$, normalized so that $\int_0^L \varphi^2(\mu, \epsilon) = 1$. Then,

$$\left(\mathfrak{L} + \frac{\mu + \beta_2}{\epsilon(\mu + \beta_2) - Q}\right)\varphi(\mu, \epsilon) = (G(\mu, \epsilon) + \mu)\varphi(\mu, \epsilon) \tag{3.14}$$

in $(0, L)$ and $\mathfrak{B}\varphi(\mu, \epsilon) = 0$. According to Remark 2.9 on page 379 of Kato [15], $\mu \mapsto \varphi(\mu, \epsilon)$ is analytic. Thus, differentiating (3.14) with respect to μ, particularizing the resulting identity at $(\mu, \epsilon) = (\lambda_p^*, 0)$ and rearranging terms yields

$$\left(\mathfrak{L} - \frac{\lambda_p^* + \beta_2}{Q} - \lambda_p^*\right)\partial_\mu \varphi(\lambda_p^*, 0) = \left[Q^{-1} + \partial_\mu G(\lambda_p^*, 0) + 1\right]\varphi(\lambda_p^*, 0) \tag{3.15}$$

in $(0, L)$ and $\mathfrak{B}\partial_\mu \varphi(\lambda_p^*, 0) = 0$. By (3.12), $\sigma_1[\mathfrak{M}, \mathfrak{B}, (0, L)] = 0$, where

$$\mathfrak{M} := \mathfrak{L} - (\lambda_p^* + \beta_2)/Q - \lambda_p^*.$$

Let $(\mathfrak{M}^*, \mathfrak{B}^*, (0, L))$ denote the adjoint of $(\mathfrak{M}, \mathfrak{B}, (0, L))$ and let $\varphi^* \gg 0$ be the principal eigenfunction associated with $\sigma_1[\mathfrak{M}^*, \mathfrak{B}^*, (0, L)] = 0$ normalized so that $\int_0^L \varphi^* \varphi(\lambda_p^*, 0) = 1$. Then, multiplying (3.15) by φ^* and integrating, we find that

$$\partial_\mu G(\lambda_p^*, 0) = -1 - 1/Q < 0,$$

which concludes the proof. □

Subsequently, we will analyze the dependence of λ_p on the diffusion rate δ and on the length of the support interval, L. Our results are based on the analysis of the dependence, with respect to d, of the principal eigenvalue $\theta(d)$, $0 < d < \infty$, of the linear eigenvalue problem

$$\begin{cases} -dw'' + w' = \theta w, & 0 < x < 1, \\ dw'(0) - w(0) = w'(1) = 0. \end{cases} \tag{3.16}$$

As the change of variable $w(x) := e^{\frac{x}{2d}} v(x)$ transforms (3.16) into

$$\begin{cases} -dv'' + \frac{1}{4d} v = \theta v, & 0 < x < 1, \\ v'(0) - \frac{1}{2d} v(0) = 0, & v'(1) + \frac{1}{2d} v(1) = 0, \end{cases} \tag{3.17}$$

it becomes apparent that

$$\theta(d) = \frac{1}{4d} + d\eta(d), \qquad d > 0, \tag{3.18}$$

where

$$\eta(d) := \sigma_1[-D^2, \mathfrak{B}(d), (0, 1)], \qquad d > 0,$$

and $\mathfrak{B}(d)$ stands for the boundary operator

$$\mathfrak{B}(d)v := \begin{cases} v'(0) - (2d)^{-1}v(0), \\ v'(1) + (2d)^{-1}v(1). \end{cases}$$

As

$$\mathfrak{B}(d) = \frac{\partial}{\partial n} + \frac{1}{2d} \qquad \text{on} \quad \partial(0,1) = \{0,1\},$$

by [2, Prop. 3.5], or [20, Prop. 8.4], $\eta(d)$ is decreasing with respect to $d > 0$. Moreover, by [2, Th. 9.1] (or [20, Th. 8.9]) and the continuous dependence of $\eta(d)$ with respect to d (see, e.g., [2, Sect. 8]), it follows that

$$\lim_{d\downarrow 0} \eta(d) = \pi^2 \qquad \text{and} \qquad \lim_{d\uparrow\infty} \eta(d) = 0,$$

i.e., rather naturally, $\eta(d)$ approximates the principal eigenvalue of the Neumann problem as $d \to \infty$, whereas it approximates the principal eigenvalue of the Dirichlet problem as $d \to 0$. In particular, this entails

$$\lim_{d\downarrow 0} \theta(d) = \infty.$$

Moreover, as $\eta(d)$ decreases, we have that

$$\theta(d) = \frac{1}{4d} + d\eta(d) < \frac{1}{4d} + d\eta(0) = \frac{1}{4d} + \pi^2 d, \qquad d > 0.$$

Proposition 2.1 of [3] sharpens the previous (rather natural) results by establishing that $d \mapsto \theta(d)$ is as well decreasing and that $\eta(d) \sim 1/d$ as $d \to \infty$. Hence,

$$\lim_{d\uparrow\infty} \theta(d) = 1.$$

Moreover, [3, Prop. 2.1] also establishes that $d \mapsto d\theta(d)$ is increasing and that

$$\frac{1}{4d} + \frac{\pi^2 d}{4} < \theta(d) < \frac{1}{4d} + \pi^2 d, \qquad \text{if } d < \pi/2,$$

though the lower estimate is not sharp, as it is only valid for sufficiently small d. More generally, let $\tau(\delta, L)$ denote the principal eigenvalue of

$$\begin{cases} -\delta\psi'' + \nu\psi' = \tau(\delta, L)\psi, & 0 < x < L, \\ \delta\psi'(0) - \nu\psi(0) = \psi'(L) = 0. \end{cases} \tag{3.19}$$

As the change of variable $x = Ly$, $w(y) = \psi(x)$, $0 < y < 1$, transforms (3.19) into

$$\begin{cases} -\dfrac{\delta}{\nu L} w'' + w' = \dfrac{\tau(\delta, L)L}{\nu} w, & 0 < y < 1, \\ \dfrac{\delta}{\nu L} w'(0) - w(0) = w'(1) = 0, \end{cases} \tag{3.20}$$

and the principal eigenvalue is unique, thanks to the previous results, from (3.18) the next result holds.

Lemma 3.1. *The following identities are satisfied*

$$\tau(\delta, L) = \frac{\nu}{L}\theta\left(\frac{\delta}{L\nu}\right) = \frac{\nu}{L}\left[\frac{L\nu}{4\delta} + \frac{\delta}{L\nu}\eta\left(\frac{\delta}{L\nu}\right)\right] = \frac{\nu^2}{4\delta} + \frac{\delta}{L^2}\eta\left(\frac{\delta}{L\nu}\right)$$

for all $\delta > 0$ and $L > 0$. Thus, the maps $\delta \mapsto \tau(\delta, L)$ and $L \mapsto \tau(\delta, L)$ are decreasing. Moreover,

$$\lim_{\delta\downarrow 0}\tau(\delta, L) = \infty = \lim_{L\downarrow 0}\tau(\delta, L), \quad \lim_{\delta\uparrow\infty}\tau(\delta, L) = \frac{\nu}{L}, \quad \lim_{L\uparrow\infty}\tau(\delta, L) = \frac{\nu^2}{4\delta}. \tag{3.21}$$

The next result provides the dependence of $\lambda_p = \lambda_p(\delta, L)$ with respect to δ in the special case when β_1 and β_2 are positive constants.

Theorem 3.4. *Suppose $\beta_1 > 0$ and $\beta_2 > 0$ are constants. Then, $\delta \mapsto \lambda_p(\delta, L)$ is decreasing. Moreover,*

$$\lambda_p(0, L) := \lim_{\delta\downarrow 0}\lambda_p(\delta, L) = \lambda_c = \alpha Q - \beta_2 \tag{3.22}$$

and, for any $\delta > 0$ and $L > 0$,

$$\lambda_p(\delta, L) = \frac{1}{2}\left\{\tau + \lambda_c + \alpha - \beta_1 - \sqrt{(\tau + \lambda_c + \alpha - \beta_1)^2 + 4\left[\alpha^2 Q + \lambda_c(\beta_1 - \alpha - \tau)\right]}\right\}, \tag{3.23}$$

where $\tau = \tau(\delta, L)$. Therefore, due to (3.21), the limit

$$\lambda_p(\infty, L) := \lim_{\delta\uparrow\infty}\lambda_p(\delta, L) < \lambda_c$$

is given through

$$\lambda_p(\infty, L) = \frac{1}{2}\left\{\frac{\nu}{L} + \lambda_c + \alpha - \beta_1 - \sqrt{\left(\frac{\nu}{L} + \lambda_c + \alpha - \beta_1\right)^2 + 4\left[\alpha^2 Q + \lambda_c(\beta_1 - \alpha - \frac{\nu}{L})\right]}\right\}.$$

Proof. By definition of λ_p, there exists a function $\psi \gg 0$, unique up to multiplicative constants, such that

$$\begin{cases} -\delta\psi'' + \nu\psi' - \beta_1\psi + \alpha + \frac{\alpha^2 Q}{\lambda_p + \beta_2 - \alpha Q} = \lambda_p\psi, & 0 < x < L, \\ \delta\psi'(0) - \nu\psi(0) = \psi'(L) = 0. \end{cases}$$

Thus, by the uniqueness of the principal eigenvalue, it becomes apparent that

$$\tau(\delta, L) = \beta_1 - \alpha + \lambda_p - \frac{\alpha^2 Q}{\lambda_p + \beta_2 - \alpha Q} = \beta_1 - \alpha + \lambda_p - \frac{\alpha^2 Q}{\lambda_p - \lambda_c}$$

or, equivalently,

$$\left(\lambda_p+\beta_1-\alpha-\tau\right)(\lambda_p-\lambda_c)-\alpha^2 Q=0.$$

Hence, λ_p must be a root of the polynomial

$$P(\lambda):=(\lambda+\beta_1-\alpha-\tau)(\lambda-\lambda_c)-\alpha^2 Q, \qquad \lambda\in\mathbb{R}.$$

As $P(\lambda_c)=-\alpha^2 Q<0$ and $\lambda_p<\lambda_c$, $P(\lambda)$ has two real roots $\lambda_-<\lambda_c<\lambda^+$ and $\lambda_p=\lambda_-$. Therefore, (3.23) holds. The formula for $\lambda_p(\infty,L)$ is a by-product from (3.21) and (3.23).

To show the monotonicity of $\delta\mapsto\lambda_p(\delta,L)$ we argue by contradiction. Suppose there are $0<\delta_1<\delta_2$ and $L>0$ such that $\lambda_p(\delta_1,L)\le\lambda_p(\delta_2,L)$. Then,

$$\begin{aligned}\tau(\delta_1,L)&=\beta_1-\alpha+\lambda_p(\delta_1,L)-\frac{\alpha^2 Q}{\lambda_p(\delta_1,L)-\lambda_c}\\ &\le\beta_1-\alpha+\lambda_p(\delta_2,L)-\frac{\alpha^2 Q}{\lambda_p(\delta_2,L)-\lambda_c}=\tau(\delta_2,L)\end{aligned}$$

which is impossible, because $\delta\mapsto\tau(\delta,L)$ is decreasing, by Lemma 3.1.

Finally, letting $\delta\downarrow 0$ in the identity

$$\tau(\delta,L)-\beta_1+\alpha-\lambda_p(\delta,L)=-\frac{\alpha^2 Q}{\lambda_p(\delta,L)-\lambda_c} \tag{3.24}$$

it becomes apparent that (3.22) holds true, because $\tau(d,L)\uparrow\infty$ as $\delta\downarrow 0$. The proof is complete. □

Similarly, the next result follows.

Theorem 3.5. *Suppose $\beta_1>0$ and $\beta_2>0$ are constants. Then, $L\mapsto\lambda_p(\delta,L)$ is decreasing. Moreover,*

$$\lambda_p(\delta,0):=\lim_{L\downarrow 0}\lambda_p(\delta,L)=\lambda_c=\alpha Q-\beta_2 \tag{3.25}$$

and the limit

$$\lambda_p(\delta,\infty):=\lim_{L\uparrow\infty}\lambda_p(\delta,L) \tag{3.26}$$

is given through

$$\begin{aligned}&\lambda_p(\delta,\infty)\\ &=\frac{1}{2}\left\{\frac{\nu^2}{4\delta}+\lambda_c+\alpha-\beta_1-\sqrt{\left(\frac{\nu^2}{4\delta}+\lambda_c+\alpha-\beta_1\right)^2+4\left[\alpha^2 Q+\lambda_c(\beta_1-\alpha-\frac{\nu^2}{4\delta})\right]}\right\}.\end{aligned}$$

Proof. The fact that $L \mapsto \lambda_p(\delta, L)$ is decreasing follows as in Theorem 3.4 from the fact that $L \mapsto \tau(\delta, L)$ is decreasing. Moreover, due to (3.21), we already know that $\lim_{L\downarrow 0} \tau(\delta, L) = \infty$. Hence, letting $L \downarrow 0$ in (3.24) yields (3.25).

Finally, as $\lambda_p(\delta, L)$ is given by (3.23), we find from the last identity of (3.21) that $\lambda_p(\delta, \infty)$ is the correct value of the limit (3.26). The proof is complete. □

In river ecology, one often has that $\nu = DL$, for some constant $D > 0$, where $L > 0$ is the length of the habitat. Consequently, it is as well of interest to ascertain how varies the principal eigenvalue λ_p as a function of the parameter $D = \nu/L$, or, equivalently, as a function of ν, if L is fixed. The next result provides us with such a dependence.

Theorem 3.6. *Suppose $\beta_1 > 0$ and $\beta_2 > 0$ are constants. Then, $D \mapsto \lambda_p(D)$ is increasing,*

$$\lim_{D\uparrow\infty} \lambda_p(D) = \lambda_c := \alpha Q - \beta_2,$$

and

$$\lambda_p(0) := \lim_{D\downarrow 0} \lambda_p(D) = \frac{1}{2}\left\{\lambda_c + \alpha - \beta_1 - \sqrt{(\lambda_c + \alpha - \beta_1)^2 + 4\left[\alpha^2 Q + \lambda_c(\beta_1 - \alpha)\right]}\right\}.$$

Proof. In terms of $D = \nu/L$, the problem (3.20) can be written in the form

$$\begin{cases} -\dfrac{\delta}{DL^2} w'' + w' = \dfrac{\tau(D)L}{\nu} w, & 0 < y < 1, \\ \dfrac{\delta}{DL^2} w'(0) - w(0) = w'(1) = 0. \end{cases}$$

Moreover, like in Theorem 3.4, we have that

$$\tau(D) = \beta_1 - \alpha + \lambda_p(D) - \frac{\alpha^2 Q}{\lambda_p(D) - \lambda_c} \tag{3.27}$$

or, equivalently,

$$\left(\lambda_p(D) + \beta_1 - \alpha - \tau\right)(\lambda_p(D) - \lambda_c) - \alpha^2 Q = 0. \tag{3.28}$$

Consequently, $\lambda_p(D)$ must be the lowest root of the polynomial

$$P_\tau(\lambda) := (\lambda + \beta_1 - \alpha - \tau)(\lambda - \lambda_c) - \alpha^2 Q, \qquad \lambda \in \mathbb{R},$$

because $P_\tau(\lambda_c) < 0$. As $\tau(D) = D\theta\left(\frac{\delta}{DL^2}\right)$ and θ is decreasing, the map $D \mapsto \tau(D)$ is increasing. Owing to (3.27), this implies that $D \mapsto \lambda_p(D)$ is also increasing. In particular, $\lambda_p(0) := \lim_{D\downarrow 0} \lambda_p(D)$ is well defined. Thanks to (3.28), $\lambda_p(0) \in \mathbb{R}$ must be the lowest root of $P_0(\lambda)$, as claimed in the statement, because $\tau(0) = 0$. Moreover, as $\lim_{D\uparrow\infty} \tau(D) = \infty$, it follows from (3.27) that $\lim_{D\uparrow\infty} \lambda_p(D) = \lambda_c$. The proof is complete. □

Remark 3.1. From the proofs of Theorems 3.4 and 3.6 we can conclude that λ_p is an increasing function of L^2/δ if $\beta_1 > 0$ and $\beta_2 > 0$ are constants. Moreover,

$$\lim_{L^2/\delta\uparrow\infty} \lambda_p = \lambda_c = \alpha Q - \beta_2 > 0; \qquad \lim_{L^2/\delta\downarrow 0+} \lambda_p = \lambda_p(0),$$

where $\lambda_p(0)$ is the lowest root of

$$(\lambda - \alpha - D + \beta_1)(\lambda - \alpha Q + \beta_2) = \alpha^2 Q,$$

which is less than $\alpha Q - \beta_2$.

4. An application

In this section we shall give some applications of the theory developed in Sections 2 and 3. We intend to incorporate the factor of vertical variation into the system in flowing habitats of [8] to study a generalized system with light limitation. Throughout this discussion, the channel is assumed to have a constant cross-sectional area A and a length L, yielding a volume V. Moreover, a flow of water enters at the upstream end ($x = 0$) with discharge F (dimensions *length*^{3}/*time*), and an equal flow leaves the downstream end ($x = L$), which is assumed to be a dam. Based on this flow, the dilution rate D (dimensions *time*$^{-1}$) is defined as F/V. Also, an advective flow within the channel is set to maintain the water balance, by transporting it with a net velocity $\nu = DL$. The reactor occupies the portion of the channel from $x = 0$ to $x = L$, where the microbial populations N_i, $i = 1, 2$, compete for the nutrient R and the light I. The competition is assumed to be purely exploitative, in the sense that the organisms simply consume the nutrient, thereby making it unavailable for a competitor. A flow of medium in the channel with velocity $\nu = DL$ in the direction of increasing x brings fresh nutrient at a constant concentration $R^{(0)}$ into the reactor, at $x = 0$, and carries medium, unutilized nutrient and organisms out of the reactor, at $x = L$. The nutrient and the organisms are assumed to diffuse throughout the vessel with the same diffusivity δ.

These assumptions lead to the next constitutive equations describing the spatial and temporal evolution of the densities $R(x, t)$, $N_1(x, t)$ and $N_2(x, t)$

$$\begin{cases} \frac{\partial R}{\partial t} = \delta \frac{\partial^2 R}{\partial x^2} - \nu \frac{\partial R}{\partial x} - q_1 f_1(R) g_1(I) N_1 - q_2 f_2(R) g_2(I) N_2 + \alpha(R_S - R), \\ \frac{\partial N_1}{\partial t} = \delta \frac{\partial^2 N_1}{\partial x^2} - \nu \frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + f_1(R) g_1(I) N_1, \\ \frac{\partial N_2}{\partial t} = \delta \frac{\partial^2 N_2}{\partial x^2} - \nu \frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(R) g_2(I) N_2, \\ \frac{\partial R_S}{\partial t} = -\alpha \frac{A}{A_S}(R_S - R) - q_1 f_1(R_S) g_1(I_S) N_{S,1} - q_2 f_2(R_S) g_1(I_S) N_{S,2}, \\ \frac{\partial N_{S,1}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,1} - N_1) + f_1(R_S) g_1(I_S) N_{S,1}, \\ \frac{\partial N_{S,2}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,2} - N_2) + f_2(R_S) g_2(I_S) N_{S,2}, \end{cases} \tag{4.1}$$

for every $(x, t) \in (0, L) \times (0, \infty)$, subject to the boundary conditions

$$\begin{cases} \nu R(0, t) - \delta \frac{\partial R}{\partial x}(0, t) = \nu R^{(0)}, \quad \frac{\partial R}{\partial x}(L, t) = 0, \\ \nu N_i(0, t) - \delta \frac{\partial N_i}{\partial x}(0, t) = 0, \quad \frac{\partial N_i}{\partial x}(L, t) = 0, \quad i = 1, 2, \end{cases} \quad t > 0, \tag{4.2}$$

and the initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, & N_i(x,0) = N_i^0(x) \geq 0, \\ R_S(x,0) = R_S^0(x) \geq 0, & N_{S,i}(x,0) = N_{S,i}^0(x) \geq 0, \end{cases} \quad 0 < x < L, \ \ i = 1,2. \tag{4.3}$$

The boundary conditions (4.2), referred to as the Danckwerts' boundary conditions by Aris [1], are often misunderstood in the literature, though they play a crucial role in the mathematical analysis of the model. A detailed sharp discussion on the role of the boundary conditions (4.2) can be found in the paper of Ballyk, Jones, and Smith [4].

In this paper, we assume that the specific growth rates $f_i(R)$ and $g_i(I)$ satisfy

$$f_i(0) = 0 \quad \text{and} \quad f_i'(R) > 0 \quad \text{for all} \quad R > 0, \qquad i = 1,2, \tag{4.4}$$

$$g_i(0) = 0 \quad \text{and} \quad g_i'(I) > 0 \quad \text{for all} \quad I > 0, \qquad i = 1,2. \tag{4.5}$$

To simplify the model as much as possible, we will assume that the vertical mixing is sufficiently strong to homogenize organisms and nutrients, i.e., we will ignore the vertical turbulent diffusion and the sinking/buoyant velocity. Then, by the Lambert–Beer law (see Huisman, Oostveen and Weissing [12] and Kirk [16], if necessary), the light intensities $I(x,t)$ and $I_S(x,t)$ take the form

$$I(x,t) = I_0\, e^{-k_0 z_m - k_1 z_m N_1(x,t) - k_2 z_m N_2(x,t)},$$
$$I_S(x,t) = I_0\, e^{-k_0 z_m - k_1 z_m N_{S,1}(x,t) - k_2 z_m N_{S,2}(x,t)},$$

where I_0 stands for the incident light intensity, z_m is the river depth, k_0 is the background turbidity that summarizes light absorption by all non-phytoplankton components, and k_i is the specific light attenuation coefficient of phytoplankton species i. The most common examples are the Monod functions, under Michaelis–Menten form,

$$f_i(R) = \frac{\mu_{\max,i} R}{K_{\mu,i} + R} \quad \text{and} \quad g_i(I) = \frac{m_i I}{a_i + I}, \qquad i = 1,2.$$

Alternatively, one might model our system replacing $f_i(R) g_i(I)$ by

$$\mathfrak{m}_i(R,I) := \min\{f_i(R), g_i(I)\}.$$

This provides us with the system

$$\begin{cases} \frac{\partial R}{\partial t} = \delta \frac{\partial^2 R}{\partial x^2} - \nu \frac{\partial R}{\partial x} - q_1 \mathfrak{m}_1(R,I) N_1 - q_2 \mathfrak{m}_2(R,I) N_2 + \alpha(R_S - R), \\ \frac{\partial N_1}{\partial t} = \delta \frac{\partial^2 N_1}{\partial x^2} - \nu \frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + \mathfrak{m}_1(R,I) N_1, \\ \frac{\partial N_2}{\partial t} = \delta \frac{\partial^2 N_2}{\partial x^2} - \nu \frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + \mathfrak{m}_2(R,I) N_2, \\ \frac{\partial R_S}{\partial t} = -\alpha \frac{A}{A_S}(R_S - R) - q_1 \mathfrak{m}_1(R_S, I_S) N_{S,1} - q_2 \mathfrak{m}_2(R_S, I_S) N_{S,2}, \\ \frac{\partial N_{S,1}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,1} - N_1) + \mathfrak{m}_1(R_S, I_S) N_{S,1}, \\ \frac{\partial N_{S,2}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,2} - N_2) + \mathfrak{m}_2(R_S, I_S) N_{S,2}, \end{cases} \tag{4.6}$$

in $(0, L) \times (0, \infty)$, which should be completed with the boundary conditions (4.2) and the initial conditions (4.3).

4.1. Dynamics of the single population model

In this section, we focus our attention on the single population model

$$\begin{cases} \frac{\partial R}{\partial t} = \delta \frac{\partial^2 R}{\partial x^2} - \nu \frac{\partial R}{\partial x} - q f(R) g(I) N + \alpha (R_S - R), \\ \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha (N_S - N) + f(R) g(I) N, \\ \frac{\partial R_S}{\partial t} = -\alpha \frac{A}{A_S} (R_S - R) - q f(R_S) g(I_S) N_S, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S} (N_S - N) + f(R_S) g(I_S) N_S, \end{cases} \tag{4.7}$$

in $(0, L) \times (0, \infty)$, under the boundary conditions

$$\begin{cases} \nu R(0,t) - \delta \frac{\partial R}{\partial x}(0,t) = \nu R^{(0)}, & \frac{\partial R}{\partial x}(L,t) = 0, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = 0, & \frac{\partial N}{\partial x}(L,t) = 0, \end{cases} \quad t > 0, \tag{4.8}$$

with initial conditions

$$\begin{cases} R(x,0) = R^0(x) \geq 0, & N(x,0) = N^0(x) \geq 0, \\ R_S(x,0) = R_S^0(x) \geq 0, & N_S(x,0) = N_S^0(x) \geq 0, \end{cases} \quad 0 < x < L. \tag{4.9}$$

In this case, the light intensities $I(x,t)$ and $I_S(x,t)$ take the form

$$I(x,t) = I_0 e^{-k_0 z_m} e^{-k z_m N(x,t)}, \qquad I_S(x,t) = I_0 e^{-k_0 z_m} e^{-k z_m N_S(x,t)}.$$

Setting

$$W(x,t) := R(x,t) + q N(x,t), \qquad W_S(x,t) := R_S(x,t) + q N_S(x,t), \tag{4.10}$$

for all $t > 0$ and $0 < x < L$, it is straightforward to see that $W(x,t)$ and $W_S(x,t)$ satisfy the evolution problem

$$\begin{cases} \frac{\partial W}{\partial t} = \delta \frac{\partial^2 W}{\partial x^2} - \nu \frac{\partial W}{\partial x} + \alpha W_S - \alpha W, & x \in (0,L),\ t > 0, \\ \frac{\partial W_S}{\partial t} = -\alpha \frac{A}{A_S} W_S + \alpha \frac{A}{A_S} W, & \\ \nu W(0,t) - \delta \frac{\partial W}{\partial x}(0,t) = \nu R^{(0)}, \quad \frac{\partial W}{\partial x}(L,t) = 0, & t > 0, \\ W(x,0) = W^0(x) \geq 0, \quad W_S(x,0) = W_S^0(x), & x \in (0,L), \end{cases} \tag{4.11}$$

where

$$W^0 := R^0 + q N^0, \qquad W_S^0 := R_S^0 + q N_S^0. \tag{4.12}$$

Adapting the arguments of Grover, Hsu and Wang [8], as well as the proof of Lemma 2.3 of Hsu, Wang and Zhao [13], the next result, describing the global dynamics of (4.11), holds. It is straightforward to check that $\left(R^{(0)}, R^{(0)}\right)$ provides us with the unique positive steady state of (4.11).

Proposition 4.1. *$\left(R^{(0)}, R^{(0)}\right)$ is the unique positive steady-state of the evolution problem (4.11), and it is a global attractor, in the sense that, for any mild solution $(W(x,t), W_S(x,t))$ of (4.11) with $\left(W^0, W_S^0\right) \in \mathcal{C}([0,L], \mathbb{R}^2)$, one has that*

$$\lim_{t\uparrow\infty} \| (W(\cdot,t), W_S(\cdot,t)) - \left(R^{(0)}, R^{(0)}\right) \|_{\mathcal{C}([0,L];\mathbb{R}^2)} = 0.$$

As an immediate consequence, we can conclude that the limiting evolution problem of (4.7)–(4.9) takes the form:

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + f(R^{(0)} - qN) g(I_0 e^{-k_0 z_m} e^{-k z_m N}) N, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + f(R^{(0)} - qN_S) g(I_0 e^{-k_0 z_m} e^{-k z_m N_S}) N_S, \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0, \qquad t > 0, \\ N(x,0) = N^0(x) \geq 0, \quad N_S(x,0) = N_S^0(x) \geq 0, \qquad x \in (0,L), \end{cases} \tag{4.13}$$

for $t > 0$ and $0 < x < L$. According to (4.10) and Proposition 4.1, it follows from (4.12) that an appropriate phase space for the problem (4.13) is the next one

$$\mathbb{X} := \left\{ (N^0, N_S^0) \in \mathcal{C}([0,L], \mathbb{R}_+^2) \mid qN^0 \leq R^{(0)}, \ qN_S^0 \leq R^{(0)} \text{ in } [0,L] \right\}. \tag{4.14}$$

Adapting the proof of Grover, Hsu and Wang [8, Prop. 3.1], the next result holds.

Proposition 4.2. *For every $\left(N^0, N_S^0\right) \in \mathbb{X}$, the evolution problem (4.13) admits a unique global mild solution*

$$(N(\cdot,t), N_0(\cdot,t)) := \left(N\left(\cdot, t; N^0, N_S^0\right), N_S\left(\cdot, t; N^0, N_S^0\right)\right), \qquad t > 0,$$

such that $(N(\cdot,t), N_0(\cdot,t)) \in \mathbb{X}$ for all $t > 0$. In other words, $\mathbb{X}$ is positively invariant by the semi-flow generated by (4.13), which will be subsequently denoted by $\Pi_t : \mathbb{X} \to \mathbb{X}$, $t > 0$.

Setting

$$\beta := f(R^{(0)}) g(I_0 e^{-k_0 z_m}) \tag{4.15}$$

and linearizing the evolution problem (4.13) at the steady state $(0,0)$, yields the cooperative system

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + \beta N, & x \in (0,L), \ t > 0, \\ \frac{\partial N_S}{\partial t} = -\alpha \frac{A}{A_S}(N_S - N) + \beta N_S, & \\ \nu N(0,t) - \delta \frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0, & t > 0, \\ N(x,0) = N^0(x) \geq 0, \ N_S(x,0) = N_S^0(x) \geq 0, & x \in (0,L). \end{cases} \tag{4.16}$$

Substituting

$$N(x,t) = e^{-\mu t}\psi(x), \qquad N_S(x,t) = e^{-\mu t}\varphi(x),$$

in (4.16), we are driven to the associated eigenvalue problem

$$\begin{cases} -\delta\psi'' + \nu\psi' + \alpha\psi - \beta\psi - \alpha\varphi = \mu\psi, & \text{in } (0,L), \\ -\alpha\frac{A}{A_S}\psi + \left(\alpha\frac{A}{A_S} - \beta\right)\varphi = \mu\varphi, & \\ \nu\psi(0) - \delta\psi'(0) = \psi'(L) = 0. \end{cases} \tag{4.17}$$

According to Theorem 2.1, under condition

$$\alpha A/A_S > \beta := f(R^{(0)})g(I_0 e^{-k_0 z_m}), \tag{4.18}$$

the eigenvalue problem (4.17) has a unique principal eigenvalue, denoted by μ^0, associated with a positive eigenvector $(\psi^0, \varphi^0) \gg 0$, which is unique up to a positive multiplicative constant.

In the sequel, we will set

$$\mathbb{X}_0 := \mathbb{X} \setminus \{(0,0)\}.$$

Then,

$$\operatorname{Int}\mathbb{X}_0 = \{(N, N_S^0) \in \mathbb{X}_0 \,:\, (N, N_S) \gg 0\}, \qquad \partial\mathbb{X}_0 = \mathbb{X}_0 \setminus \operatorname{Int} X_0.$$

Theorem 4.1. *Suppose (4.18) holds and let μ^0 denote the (unique) principal eigenvalue of (4.17). For any $(N^0, N_S^0) \in \mathbb{X}$, let $(N(\cdot,t), N_S(\cdot,t)) = \Pi_t(N^0, N_S^0)$, $t > 0$, be the unique mild solution of (4.13). Then, the following assertions are true:*

(i) *If $\mu^0 > 0$, then $\lim_{t\to\infty}(N(\cdot,t), N_S(\cdot,t)) = (0,0)$ uniformly in $[0,L]$;*

(ii) *If $\mu^0 < 0$, then, the problem (4.13) admits a unique positive steady state, denoted by (N^*, N_S^*), and, for every $(N^0, N_S^0) \in \mathbb{X}_0$, one has that*

$$\lim_{t\to\infty}(N(\cdot,t), N_S(\cdot,t)) = (N^*, N_S^*) \quad \textit{uniformly in } [0,L].$$

Proof. Suppose $\mu^0 > 0$. Then, it follows from (4.13) that

$$\begin{cases} \frac{\partial N}{\partial t} \le \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + \beta N, & x \in (0,L),\ t > 0, \\ \frac{\partial N_S}{\partial t} \le -\alpha\frac{A}{A_S}(N_S - N) + \beta N_S, & \\ \nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \frac{\partial N}{\partial x}(L,t) = 0, & t > 0, \\ N(x,0) = N^0(x) \ge 0,\ N_S(x,0) = N_S^0(x) \ge 0, & x \in (0,L). \end{cases}$$

Moreover, since $(\psi^0, \varphi^0) \gg 0$, for any given $(N^0, N_S^0) \in \mathbb{X}$, there is a constant $a > 0$ such that $(N^0, N_S^0) \le a(\psi^0, \varphi^0)$ in $[0,L]$. As $ae^{-\mu^0 t}(\psi^0, \varphi^0)$, $t > 0$, solves (4.16) with initial data

$a(\psi^0, \varphi^0)$, from the parabolic maximum principle it is apparent that

$$(N(\cdot,t), N_S(\cdot,t)) \le a e^{-\mu^0 t}(\psi^0, \varphi^0) \quad \text{in} \quad [0, L] \quad \text{for all } t > 0,$$

which entails assertion (i).

Subsequently, we assume that $\mu^0 < 0$. Then, by Theorem 2.1, as soon as

$$\epsilon_0 > 0, \qquad \alpha A/A_S > \beta - \epsilon_0, \tag{4.19}$$

the linear eigenvalue problem

$$\begin{cases} -\mu\psi = \delta\psi'' - \nu\psi' + \alpha(\varphi - \psi) + (\beta - \epsilon_0)\psi, & \\ -\mu\varphi = -\alpha\frac{A}{A_S}(\varphi - \psi) + (\beta - \epsilon_0)\varphi, & \text{in } (0, L), \\ \nu\psi(0) - \delta\psi'(0) = \psi'(L) = 0, & \end{cases} \tag{4.20}$$

possesses a unique principal eigenvalue, denoted by $\mu^0_{\epsilon_0}$. According to Theorem 3.1, $\mu^0 < \mu_{\epsilon_0}$, because $\beta - \epsilon_0 < \beta$. Moreover, by adapting the argument of the proof of Theorem 3.3, it is easy to see that $\epsilon \mapsto \mu_\epsilon$ is a real analytic function. Hence, for sufficiently small $\epsilon_0 > 0$, (4.19) and $\mu^0_{\epsilon_0} < 0$ hold. Let $(\psi^0_{\epsilon_0}, \varphi^0_{\epsilon_0}) \gg 0$ be an eigenfunction associated with $\mu^0_{\epsilon_0}$, and pick $(N^0, N^0_S) \in \mathbb{X}_0$. By the parabolic strong maximum principle (see Nirenberg [24], if necessary), $(N(\cdot,t), N_S(\cdot,t)) \gg 0$ for all $t > 0$. In other words,

$$\Pi_t(\mathbb{X}_0) \subseteq \operatorname{Int}\mathbb{X}_0 \qquad \text{for all} \quad t > 0.$$

On the other hand, since

$$\lim_{N\to 0} f(R^{(0)} - qN)g(I_0 e^{-k_0 z_m} e^{-k z_m N}) = f(R^{(0)})g(I_0 e^{-k_0 z_m}) = \beta,$$
$$\lim_{N_S\to 0} f(R^{(0)} - qN_S)g(I_0 e^{-k_0 z_m} e^{-k z_m N_S}) = f(R^{(0)})g(I_0 e^{-k_0 z_m}) = \beta,$$

there exists $\sigma_0 >$ such that

$$\begin{aligned} f(R^{(0)} - qN)g(I_0 e^{-k_0 z_m} e^{-k z_m N}) &> \beta - \epsilon_0, \\ f(R^{(0)} - qN_S)g(I_0 e^{-k_0 z_m} e^{-k z_m N_S}) &> \beta - \epsilon_0, \end{aligned} \qquad \text{if} \quad \|(N, N_S)\| < \sigma_0, \tag{4.21}$$

which entails

$$\limsup_{t\to\infty} \|\Pi_t(N^0, N^0_S) - (0,0)\| \ge \sigma_0 \quad \text{for all } (N^0, N^0_S) \in \mathbb{X}_0 \tag{4.22}$$

and shows that $(0, 0)$ is a *uniform weak repeller* for the evolution problem (4.13). Indeed, suppose (by contradiction) that there is $(N^0, N^0_S) \in \mathbb{X}_0$ such that

$$\limsup_{t\to\infty} \|\Pi_t(N^0, N^0_S) - (0,0)\| < \sigma_0. \tag{4.23}$$

Then, if follows from (4.13) and (4.21) that there exists $t_0 > 0$ such that

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \alpha(N_S - N) + (\beta - \epsilon_0)N, & x \in (0, L), \quad t \geq t_0, \\ \frac{\partial N_S}{\partial t} \geq -\alpha \frac{A}{A_S}(N_S - N) + (\beta - \epsilon_0)N_S, & \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \frac{\partial N}{\partial x}(L, t) = 0, & t \geq t_0. \end{cases} \tag{4.24}$$

As $(N^0, N_S^0) \in \mathbb{X}_0$, we have that

$$\Pi_{t_0}(N^0, N_S^0) = \left(N\left(\cdot, t_0; N^0, N_S^0\right), N_S\left(\cdot, t_0; N^0, N_S^0\right)\right) \gg 0 \qquad \text{for all } x \in [0, L]$$

and hence, there is a constant $b > 0$ such that

$$\Pi_{t_0}(N^0, N_S^0) > b(\psi_{\epsilon_0}^0, \varphi_{\epsilon_0}^0) \qquad \text{in} \quad [0, L].$$

Consequently, we find from the parabolic maximum principle that

$$\Pi_t(N^0, N_S^0) = \left(N\left(\cdot, t; N^0, N_S^0\right), N_S\left(\cdot, t; N^0, N_S^0\right)\right) \geq b e^{-\mu_{\epsilon_0}^0 (t - t_0)} \left(\psi_{\epsilon_0}^0, \varphi_{\epsilon_0}^0\right)$$

in $[0, L]$ for all $t \geq t_0$. Since $\mu_{\epsilon_0}^0 < 0$, $\left(N\left(\cdot, t; N^0, N_S^0\right), N_S\left(\cdot, t; N^0, N_S^0\right)\right)$, $t > 0$, is unbounded, which contradicts (4.23) and ends the proof of (4.22).

Subsequently, we consider the kinetics of (4.13), $\mathfrak{F} := (F, F_S) : \mathbb{R}^2 \to \mathbb{R}^2$, with

$$F(N, N_S) := \alpha(N_S - N) + f(R^{(0)} - qN)g(I_0 e^{-k_0 z_m} e^{-k z_m N})N,$$
$$F_S(N, N_S) := -\alpha \frac{A}{A_S}(N_S - N) + f(R^{(0)} - qN_S)g(I_0 e^{-k_0 z_m} e^{-k z_m N_S})N_S.$$

By (4.18), it is easy to see that there exists a real number $r > 0$ such that

$$\frac{\partial F_S(N, N_S)}{\partial N_S} \leq -r < 0 \qquad \text{for all} \quad (N, N_S) \in \left[0, R^{(0)}/q\right] \times \left[0, R^{(0)}/q\right].$$

By Proposition 4.2, arguing as in the proof of Lemma 4.1 and Theorem 4.1 of Hsu, Wang and Zhao [13], it becomes apparent that the semigroup Π_t, $t > 0$, has a global compact attractor in $\mathbb{X}$.

Let $\rho : \mathbb{X} \to [0, \infty)$ be the continuous function defined by

$$\rho(N^0, N_S^0) := \min\left\{ \min_{x \in [0, L]} N^0(x), \min_{x \in [0, L]} N_S^0(x) \right\} \qquad \text{for all} \quad (N^0, N_S^0) \in \mathbb{X}.$$

It is easy to see that $\rho^{-1}(0, \infty) \subseteq \mathbb{X}_0$ and that $\rho\left(\Pi_t(N^0, N_S^0)\right) > 0$ for all $t > 0$ if either $\rho(N^0, N_S^0) > 0$ or $(N^0, N_S^0) \in \mathbb{X}_0$ with $\rho(N^0, N_S^0) = 0$. Thus, ρ is a *generalized distance function* for the evolution operator $\Pi_t : \mathbb{X} \to \mathbb{X}$ (see, e.g., Smith and Zhao [28]). From these features, one can infer that the ω-limit set $\omega(N^0, N_S^0)$ of any point

$$(N^0, N_S^0) \in M_\partial := \left\{(N^0, N_S^0) \in \partial\mathbb{X}_0 \;:\; \Pi_t(N^0, N_S^0) \in \partial\mathbb{X}_0 \quad \forall\, t > 0\right\},$$

must be $\{(0,0)\}$. Thus, any forward orbit of Π_t in M_∂ converges to $(0,0)$, which is isolated in $\mathbb{X}$, and $W^s(0,0) \cap \mathbb{X}_0 = \emptyset$, where $W^s(0,0)$ stands for the stable manifold of $(0,0)$. As it is obvious that there is no cycle in M_∂ linking $(0,0)$ with $(0,0)$, Theorem 3 of Smith and Zhao [28] shows that there is a constant $\eta > 0$ such that

$$\min_{Q\in\omega(N^0,N_S^0)} \rho(Q) > \eta \qquad \text{for all} \quad (N^0, N_S^0) \in \mathbb{X}_0.$$

Therefore, by Theorem 3.8 of Magal and Zhao [23], $\Pi_t : \mathbb{X}_0 \to \mathbb{X}_0$ admits a global attractor A_0.

On the other hand, as the Jacobian matrix of $\mathfrak{F}(N, N_S)$ is cooperative and irreducible for any $(N, N_S) \in [0, R^{(0)}/q] \times [0, R^{(0)}/q]$, and $\mathfrak{F}(N, N_S)$ is strongly sub-homogeneous in $[0, R^{(0)}/q] \times [0, R^{(0)}/q]$, in the sense that

$$\mathfrak{F}(\tau N, \tau N_S) \gg \tau\mathfrak{F}(N, N_S)$$

for all $\tau \in (0,1)$ and $(N, N_S) \in (0, R^{(0)}/q] \times (0, R^{(0)}/q]$, the evolution operator $\Pi_t : \mathbb{X} \to \mathbb{X}$ is a strongly monotone and strictly sub-homogeneous semi-flow in $\mathbb{X}$ (see, e.g., Section 2.3 of Zhao [30]). As $A_0 \subset \mathbb{X}_0$ and $A_0 = \Pi_t(A_0)$ for all $t > 0$, necessarily $A_0 \subset \operatorname{Int}\left(\mathcal{C}\left([0,L], \mathbb{R}^2_+\right)\right)$. Therefore, applying Theorem 2.3.2 of [30] with $K = A_0$, it becomes apparent that A_0 consists of a single point $(N^*, N_S^*) \gg 0$. This ends the proof of part (ii). □

Remark 4.1. By Theorem 4.1 and the method of chain transitive sets (see, e.g., Section 1.2 of Zhao [30]), one can also derive a threshold type result on the global dynamics of the single species model (4.7)–(4.9).

4.2. Dynamics of the two-populations model

This section analyzes the dynamics of the evolution problem (4.1)–(4.3). Setting

$$\mathcal{W}(x,t) := R(x,t) + q_1 N_1(x,t) + q_2 N_2(x,t),$$
$$\mathcal{W}_S(x,t) := R_S(x,t) + q_1 N_{S,1}(x,t) + q_2 N_{S,2}(x,t),$$

and substituting in (4.1)–(4.3), it becomes apparent that $(\mathcal{W}, \mathcal{W}_S)$ solves (4.11). Thus, due to Lemma 4.1, $(\mathcal{W}(\cdot,0), \mathcal{W}_S(\cdot,0)) \in \mathcal{C}([0,L], \mathbb{R}^2)$ implies

$$\lim_{t\to\infty} (\mathcal{W}(\cdot,t), \mathcal{W}_S(\cdot,t)) = (R^{(0)}, R^{(0)}) \quad \text{uniformly in} \quad [0,L].$$

Consequently, the limiting system of (4.1)–(4.3) takes the form

$$\begin{cases} \frac{\partial N_1}{\partial t} = \delta \frac{\partial^2 N_1}{\partial x^2} - \nu \frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) \\ \qquad + f_1(R^{(0)} - q_1 N_1 - q_2 N_2) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_1} e^{-k_2 z_m N_2}) N_1, \\ \frac{\partial N_{S,1}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,1} - N_1) \\ \qquad + f_1(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}}) N_{S,1}, \\ \frac{\partial N_2}{\partial t} = \delta \frac{\partial^2 N_2}{\partial x^2} - \nu \frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) \\ \qquad + f_2(R^{(0)} - q_1 N_1 - q_2 N_2) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_1} e^{-k_2 z_m N_2}) N_2, \\ \frac{\partial N_{S,2}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,2} - N_2) \\ \qquad + f_2(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}}) N_{S,2}, \end{cases} \tag{4.25}$$

in $(x, t) \in (0, L) \times (0, \infty)$, with boundary and initial conditions

$$\begin{cases} \nu N_i(0,t) - \delta \frac{\partial N_i}{\partial x}(0,t) = \frac{\partial N_i}{\partial x}(L,t) = 0, & t > 0, \\ N_i(x,0) = N_i^0(x) \geq 0, \ N_{S,i}(x,0) = N_{S,i}^0(x) \geq 0, & 0 < x < L, \end{cases} \quad i = 1, 2. \tag{4.26}$$

From the biological point of view, the natural phase space for (4.25)–(4.26) is

$$\mathbb{Y} := \left\{ (N_1^0, N_{S,1}^0, N_2^0, N_{S,2}^0) \in \mathcal{C}([0,L], \mathbb{R}_+^4) : \begin{cases} q_1 N_1^0 + q_2 N_2^0 \leq R^{(0)}, \\ q_1 N_{S,1}^0 + q_2 N_{S,2}^0 \leq R^{(0)}, \end{cases} \text{in } [0, L] \right\}.$$

The next result can be proved by similar arguments as in Proposition 3.1 of Grover, Hsu and Wang [8].

Proposition 4.3. *For every* $P := \left(N_1^0, N_{S,1}^0, N_2^0, N_{S,2}^0\right) \in \mathbb{Y}$, *the evolution problem* (4.25)–(4.26) *admits a unique global mild solution*

$$\left(N_1(\cdot, t; P), N_{S,1}(\cdot, t; P), N_2(\cdot, t; P), N_{S,2}(\cdot, t; P)\right), \qquad t > 0,$$

such that

$$\left(N_1(\cdot, t; P), N_{S,1}(\cdot, t; P), N_2(\cdot, t; P), N_{S,2}(\cdot, t; P)\right) \in \mathbb{Y}$$

for all $t > 0$. *In other words, the phase space* $\mathbb{Y}$ *is positively invariant under the semi-flow generated by the problem* (4.25)–(4.26).

Naturally, Theorem 4.1 can be applied to each of the two sub-systems obtained from (4.25)–(4.26) by setting to $(0, 0)$ any of the two ordered pairs $(N_1, N_{S,1})$, or $(N_2, N_{S,2})$. Suppose

$$\alpha \frac{A}{A_S} > \beta_i := f_i(R^{(0)}) g(I_0 e^{-k_0 z_m}), \quad i = 1, 2. \tag{4.27}$$

Then, owing to Theorem 2.1, the problem (4.17) with $\beta = \beta_i$, $i = 1, 2$, possesses a unique principal eigenvalue μ_i^0, and we can conclude that the problem (4.25)–(4.26) admits the following types of steady states:

(a) The *trivial solution* $\hat{0} := (0, 0, 0, 0)$, which exists always;
(b) The *semi-trivial solution* $E_1 := (N_1^*, N_{S,1}^*, 0, 0)$, which exists if, and only if, $\mu_1^0 < 0$;
(c) The *semi-trivial solution* $E_2 := (0, 0, N_2^*, N_{S,2}^*)$, which exists if, and only if, $\mu_2^0 < 0$;
(d) The *coexistence states*, which are solutions with the four components positive, whose existence is not guaranteed yet.

Here, we are denoting by $(N_i^*, N_{S,i}^*)$ the unique positive steady-state solution of (4.13) with $f = f_i$, $q = q_i$ and $k = k_i$, $i = 1, 2$. The two organisms can coexist if a coexistence state exists.

Linearizing the problem (4.25)–(4.26) at the steady state $E_1 := (N_1^*, N_{S,1}^*, 0, 0)$, one gets the following cooperative system that is decoupled from the remaining equations

$$\begin{cases} \frac{\partial N_2}{\partial t} = \delta \frac{\partial^2 N_2}{\partial x^2} - \nu \frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(R^{(0)} - q_1 N_1^*) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_1^*}) N_2, \\ \frac{\partial N_{S,2}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,2} - N_2) + f_2(R^{(0)} - q_1 N_{S,1}^*) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}^*}) N_{S,2}, \\ \nu N_2(0,t) - \delta \frac{\partial N_2}{\partial x}(0,t) = \frac{\partial N_2}{\partial x}(L,t) = 0, \quad t > 0, \\ N_2(x,0) = N_2^0(x) \geq 0, \quad N_{S,2}(x,0) = N_{S,2}^0(x) \geq 0, \quad x \in (0,L), \end{cases}$$

in $(x,t) \in (0,L) \times (0,\infty)$. Thus, setting

$$\beta_{1,1}(x) := f_2(R^{(0)} - q_1 N_1^*(x)) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_1^*(x)})$$

$$\beta_{1,2}(x) := f_2(R^{(0)} - q_1 N_{S,1}^*(x)) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}^*(x)})$$

for every $x \in (0, L)$, and substituting $N_2(x,t) = e^{-\Lambda_1 t}\psi(x)$ and $N_{S,2}(x,t) = e^{-\Lambda_1 t}\varphi(x)$ into the previous linearized problem, one obtains the associated eigenvalue problem

$$\begin{cases} -\delta\psi'' + \nu\psi' + \alpha\psi - \beta_{1,1}(x)\psi - \alpha\varphi = \Lambda_1\psi, \\ -\alpha\frac{A}{A_S}\psi + \left(\alpha\frac{A}{A_S} - \beta_{1,2}(x)\right)\varphi = \Lambda_1\varphi, \\ \nu\psi(0) - \delta\psi'(0) = \psi'(L) = 0. \end{cases} \quad \text{in } (0,L), \tag{4.28}$$

According to Theorem 2.1, the linear eigenvalue problem (4.28) has a principal eigenvalue, denoted by Λ_1^0, provided that

$$\alpha\frac{A}{A_S} > f_2(R^{(0)} - q_1 N_{S,1}^*(x)) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}^*(x)}) \quad \text{for all} \quad x \in [0,L]. \tag{4.29}$$

Similarly, linearizing the problem (4.25)–(4.26) at the steady state solution $E_2 := (0, 0, N_2^*, N_{S,2}^*)$, one is driven to the next cooperative system, which is uncoupled with respect to the remaining equations

$$\begin{cases} \frac{\partial N_1}{\partial t} = \delta \frac{\partial^2 N_1}{\partial x^2} - \nu \frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + f_1(R^{(0)} - q_2 N_2^*) g(I_0 e^{-k_0 z_m} e^{-k_2 z_m N_2^*}) N_1, \\ \frac{\partial N_{S,1}}{\partial t} = -\alpha \frac{A}{A_S}(N_{S,1} - N_1) + f_1(R^{(0)} - q_2 N_{S,2}^*) g(I_0 e^{-k_0 z_m} e^{-k_2 z_m N_{S,2}^*}) N_{S,1}, \\ \nu N_1(0,t) - \delta \frac{\partial N_1}{\partial x}(0,t) = \frac{\partial N_1}{\partial x}(L,t) = 0, \quad t > 0, \\ N_1(x,0) = N_1^0(x) \geq 0, \quad N_{S,1}(x,0) = N_{S,1}^0(x) \geq 0, \quad x \in (0,L). \end{cases}$$

Thus, setting

$$\beta_{2,1}(x) := f_1(R^{(0)} - q_2 N_2^*(x)) g(I_0 e^{-k_0 z_m} e^{-k_2 z_m N_2^*(x)})$$
$$\beta_{2,2}(x) := f_1(R^{(0)} - q_2 N_{S,2}^*(x)) g(I_0 e^{-k_0 z_m} e^{-k_2 z_m N_{S,2}^*(x)})$$

for every $x \in (0, L)$, and substituting $N_1(x,t) = e^{-\Lambda_2 t}\psi(x)$ and $N_{S,1}(x,t) = e^{-\Lambda_2 t}\varphi(x)$ into the previous linearized problem, one gets

$$\begin{cases} -\delta\psi'' + \nu\psi' + \alpha\psi - \beta_{2,1}(x)\psi - \alpha\varphi = \Lambda_2\psi, \\ -\alpha\frac{A}{A_S}\psi + \left(\alpha\frac{A}{A_S} - \beta_{2,2}(x)\right)\varphi = \Lambda_2\varphi, \\ \nu\psi(0) - \delta\psi'(0) = \psi'(L) = 0. \end{cases} \quad \text{in } (0,L), \tag{4.30}$$

By Theorem 2.1, the eigenvalue problem (4.30) has a principal eigenvalue, denoted by Λ_2^0, provided that

$$\alpha\frac{A}{A_S} > f_1(R^{(0)} - q_2 N_{S,2}^*(x)) g(I_0 e^{-k_0 z_m} e^{-k_2 z_m N_{S,2}^*(x)}) \qquad \text{for all} \quad [0, L]. \tag{4.31}$$

Remark 4.2. It should be noted that:

(i) The conditions (4.27) imply (4.29) and (4.31);
(ii) Thanks to Theorem 3.1, $\Lambda_1^0 > \mu_2^0$ and $\Lambda_2^0 > \mu_1^0$.

As two of the differential equations of the evolution problem (4.25)–(4.26) have no diffusion terms, its associated semi-flow Φ_t, $t > 0$, is not compact. Let

$$H_1(N_1, N_{S,1}, N_2, N_{S,2}) \quad \text{and} \quad H_2(N_1, N_{S,1}, N_2, N_{S,2})$$

denote the reaction terms of the second and fourth equations of system (4.25), respectively. Subsequently, we will impose that there is a constant $r > 0$ such that, for every $(N_1, N_{S,1}, N_2, N_{S,2}) \in \mathbb{Y}$,

$$\mathbf{x}^T \mathcal{M}(N_1, N_{S,1}, N_2, N_{S,2})\mathbf{x} \leq -r\,\mathbf{x}^T\mathbf{x} \qquad \text{for all} \quad \mathbf{x} \in \mathbb{R}^2, \tag{4.32}$$

where

$$\mathcal{M}(N_1, N_{S,1}, N_2, N_{S,2}) := \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix},$$

with

$$
\begin{aligned}
m_{11} &:= \frac{\partial H_1(N_1, N_{S,1}, N_2, N_{S,2})}{\partial N_{S,1}} \\
&= -\alpha \frac{A}{A_S} + f_1(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}}) \\
&+ \frac{\partial [f_1(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}})]}{\partial N_{S,1}} N_{S,1}, \\
m_{21} &:= \frac{\partial H_2(N_1, N_{S,1}, N_2, N_{S,2})}{\partial N_{S,1}} \\
&= \frac{\partial [f_2(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}})]}{\partial N_{S,1}} N_{S,2}, \\
m_{12} &= \frac{\partial H_1(N_1, N_{S,1}, N_2, N_{S,2})}{\partial N_{S,2}} \\
&= \frac{\partial [f_1(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}})]}{\partial N_{S,2}} N_{S,1}, \\
m_{22} &:= \frac{\partial H_2(N_1, N_{S,1}, N_2, N_{S,2})}{\partial N_{S,2}} \\
&= -\alpha \frac{A}{A_S} + f_2(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}}) \\
&+ \frac{\partial [f_2(R^{(0)} - q_1 N_{S,1} - q_2 N_{S,2}) g(I_0 e^{-k_0 z_m} e^{-k_1 z_m N_{S,1}} e^{-k_2 z_m N_{S,2}})]}{\partial N_{S,2}} N_{S,2}.
\end{aligned}
$$

Remark 4.3. It is easy to see that (4.32) holds for sufficiently large $\alpha A/A_S$.

Consider the cone $K := \mathcal{C}([0, L], \mathbb{R}^2_+) \times (-\mathcal{C}([0, L], \mathbb{R}^2_+))$ and denote by $\leq_K$ its induced order. Then, by the parabolic maximum principle, the Poincaré map $\Phi_t : \mathbb{Y} \to \mathbb{Y}$, $t > 0$, generated by (4.25)–(4.26) is monotone with respect to the partial order $\leq_K$, as discussed by Smith [27].

As usual, for any given $P_1, P_2 \in \mathbb{Y}$ with $P_1 \leq_K P_2$, we define the K-order interval

$$
[P_1, P_2]_K := \{P \in \mathbb{Y} : \ P_1 \leq_K P \leq_K P_2\},
$$

and consider the subsets of the phase space

$$
\mathbb{Y}_0 := \left\{(N_1, N_{S,1}, N_2, N_{S,2}) \in \mathbb{Y} : \ (N_j, N_{S,j}) \neq (0,0), \ j = 1, 2\right\}
$$

and $\partial \mathbb{Y}_0 := \mathbb{Y}_0 \setminus \operatorname{Int} \mathbb{Y}_0$. The main result of this section reads as follows.

Theorem 4.2. *Suppose (4.27) and (4.32) hold. Then, the following assertions are true:*

(i) *If $\Lambda_i^0 < 0$, $i = 1, 2$, then, the problem (4.25)–(4.26) admits a minimal coexistence state and a maximal coexistence state, with respect to the order $\leq_K$,*

$$
E^- := (\underline{N}_1, \underline{N}_{S,1}, \overline{N}_2, \overline{N}_{S,2}) \leq_K E^+ := (\overline{N}_1, \overline{N}_{S,1}, \underline{N}_2, \underline{N}_{S,2}),
$$

such that

$$\lim_{t\to\infty} d\left(\Phi_t(P), [E^-, E^+]_K\right) = 0 \qquad \textit{for all} \quad P \in \mathbb{Y}_0.$$

(ii) *If* $\mu_i^0 > 0$ *and* $\Lambda_i^0 > 0$, $i = 1, 2$, *then, the problem* (4.25)–(4.26) *admits, at least, one coexistence state in* $\mathbb{Y}$.

Proof. By (4.32), adapting the arguments of the proof of Theorem 4.1 of Hsu, Wang and Zhao, it is apparent that Φ_t admits a global attractor on $\mathbb{Y}$. Moreover, it is easy to see that the semi-trivial steady states E_1 and E_2 of (4.25)–(4.26) both exist and are linearly unstable if $\Lambda_i^0 < 0$, $i = 1, 2$, whereas both are locally asymptotically stable if $\mu_i^0 > 0$ and $\Lambda_i^0 > 0$, $i = 1, 2$. Theorem B and Corollary 1 of Hsu, Smith and Waltman complete the proof. □

Remark 4.4. By Theorem 4.2 and the method of chain transitive sets, as illustrated in Section 5 of Hsu, Wang and Zhao [13], one can lift the dynamics of the problem (4.25)–(4.26) to the full system (4.1)–(4.3).

Actually, as discussed by Hess [11] for the classical periodic–parabolic Lotka–Volterra models, in case (i) of Theorem 4.2 the problem is *compressive*. Moreover, as for each $i = 1, 2$, the semi-trivial positive steady state E_i is linearly asymptotically stable if, and only if, $\Lambda_i^0 > 0$ and linearly unstable if, and only if, $\Lambda_i^0 < 0$, one can easily adapt the techniques of Eilbeck et al. [6] and Furter and López-Gómez [7] to construct examples where one of the semi-trivial solutions, e.g., E_1, is linearly asymptotically stable, while E_2 is linearly unstable. In such cases, according to the fixed point index calculations of López-Gómez [18] and Theorem 5.1 of López-Gómez and Sabina de Lis [22], it is well known that the problem must exhibit at least two coexistence states. Actually, one of them should be linearly stable, the minimal one, while some other must be linearly unstable. In these situations, the problem should admit an even number of coexistence states, at least generically.

5. Discussion

This paper has analyzed the competition between two microbial species in a flow-reactor habitat in the general case when the growth of the species depends on nutrients and light. The mathematical model consists of a system of partial differential equations coupled with a system of ordinary differential equations, which extends a previous model introduced by Grover, Hsu and Wang [8], where the light factor was not incorporated into the model setting.

Essentially, the mathematical analysis of this paper is divided in three parts. First, we have established the existence and uniqueness of the principal eigenvalue for a certain linear eigenvalue problem whose sign determines whether or not the trivial solution of the single species model is linearly asymptotically stable. It turns out that the sign of the principal eigenvalue is pivotal to ascertain the dynamics of these models. Then, we have analyzed exhaustively the dependence of the principal eigenvalue with respect to the most significative parameters involved in the formulation of the single species model. Finally, we have characterized the dynamics of the single species model through the sign of the principal eigenvalue of the linearization at the trivial solutions, and have established the existence of coexistence states in the competing species model through the sign of the principal eigenvalues of the semi-trivial solutions of the model.

It turns out that the model possesses a coexistence state if both semi-trivial states are linearly unstable, or both are linearly stable, and that the species are permanent if both semi-trivial states are linearly unstable (see Theorem 4.2). In order to establish these results we have assumed the general reproductive rate to be given through the product of an increasing function of the nutrient concentration with another increasing function of the light intensity. As far as concerns with the single phytoplankton species dynamics, we have established that the species is permanent if, and only if, the trivial solution is linearly unstable, which can be measured through the sign of the principal eigenvalue of its linearization (see Theorem 4.1).

In flow-reactor habitats, the development of longitudinal patterns for the steady states on flow conditions is often determined from the dimensionless Péclet number, $P_e := DL^2/\delta$ (see, e.g., Grover et al. [9]). For higher critical values of the Péclet number, algal populations were predicted to be washed out by rapid flow. According to the analysis carried out in this paper, it also becomes apparent how the persistence of the single species depends on the transport characteristics of the habitat, measured by the diffusivity δ and the advection ν, as well as on the exchanging rate between the main channel and the storage zone, measured by α.

According to Theorems 3.1, 3.4 and 3.5, the principal eigenvalue μ^0 of the linearized system at the trivial solution is decreasing with respect to δ, α and the reproductive rate of the species, while it is increasing with respect to $\nu := DL$, D, L and the ratio A/A_S. As a by-product, thanks to Theorem 4.1, it becomes apparent that the following situations will indeed facilitate the persistence of planktonic algae in flowing habitats: the larger δ, the larger α, the larger reproductive rate, the smaller D, the smaller L and the smaller A/A_S.

This paper has also determined the asymptotic behavior of the principal eigenvalue μ^0 for sufficiently large and sufficiently small positive parameters. Our results enable us to ascertain, for example, the critical diffusion rate, the critical advection rate and the critical habitat length. Indeed, one can determine the critical size of the diffusion rate δ_c, or the critical habitat length L_c, or the critical dilution rate D_c, so that the phytoplankton is driven to extinction if $L > L_c$, $D > D_c$, or $\delta < \delta_c$ (see Theorems 3.4, 3.5 and 3.6).

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