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Target reproduction numbers for reaction-diffusion population models

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Abstract A very important population threshold quantity is the target reproduction number, which is a measure of control effort required for a target prevention, intervention or control. This concept, as a generalization of type reproduction number, was first introduced in [32] for nonnegative matrices with immediate applications to compartmental population models of ordinary differential equations. The current paper is devoted to the study of all target reproduction numbers for reaction-diffusion population models with compartmental structure. It turns out that the target reproduction number can be regarded as the basic reproduction number of a modified system, where the state of newborn individuals is limited to the target control set and the offspring from the non-target set is regarded as a part of the transition. In other words, the target reproduction number can be interpreted as the expected number of offspring in a specific target set that a primary newborn individual of the same set would produce during its lifetime. We also characterize the target reproduction number so that it can be easily computed numerically for reaction-diffusion models. At the end, we demonstrate our theoretical observations using two examples.

Keywords Target reproduction number · Reaction-diffusion model · Positive operator · Population control

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1 Introduction

The basic reproduction number (or ratio) R_0 is an important concept in population biology. As a threshold quantity for population dynamics, it is unquestionably one of the most valuable mathematical ideas brought to theoretical ecology and epidemiology. Original development of this concept can be traced back to the work of Böckh [5] in 1886 on some demographic data of Berlin, and a series of research on demography by Sharp and Lotka [31] in 1911, Dublin and Lotka [8] in 1925 and Kuczynski [21] in 1928. Meanwhile, R_0 was studied independently in epidemiology for vector-born diseases [9, 26, 29] and directly-transmitted human diseases [6, 13, 20]. In epidemiology, the basic reproduction number R_0 can be interpreted as the expected number of secondary infections produced by a primary infected individual during its infectious period in an otherwise susceptible population. The systematic research of R_0 in epidemiology started with the celebrated work of Diekmann, Heesterbeek and Metz [7], in which R_0 was established for structured populations via the next generation matrix approach. The theory of R_0 has been greatly developed for compartmental models of ordinary differential equations [34], population models in a periodic environment [1–3,37] and an almost periodic environment [35], infinite-dimensional population structure and time heterogeneity [33, 38], and periodic abstract functional differential equations [24, 41]. Inaba [16] gave a new definition of R_0 for structured populations in heterogeneous environments based on the generation evolution operator, which unifies the previous definitions in [1, 7]. More recently, he showed that this R_0 serves as a threshold value for population extinction and persistence in time-heterogeneous environments [18].

If a population control strategy (e.g., disease control or population protection) is targeted at specific types of the individuals instead of the entire heterogeneous population, R_0 may not be the right quantity to study, and moreover, it is crucial to know in practice whether that strategy works. To address this question, Roberts and Heesterbreek [12, 28] proposed and developed the concept of the type reproduction number T for nonnegative matrices, particularly in the context of mathematical epidemiology, to determine the control effort needed to eliminate the infection. T measures the average number of secondary infection of the target types that a primary case of the same types would produce during the course of infection. In [28], Roberts and Heesterbeek showed that T and R_0 stay on the same side of the unity when T is well-defined, and that $1 - \frac{1}{T}$ typically represents the fraction of the target host required to be controlled out of the whole population for eradicating the disease. Inaba and Nishiura [19] also extended the idea of type reproduction number to the state-reproduction number for the non-birth state of target host types (where newborns couldn't be reproduced). Recently, Inaba [17] used the generation evolution operator approach to give a general definition of T for continuously structured populations in heterogeneous environments. Shuai at al. [32] extended the type reproduction number T to the target reproduction number $T_{\mathcal{M}}$, in which control effort can be aimed at the interactions between types

rather than specific types alone. Lewis et al. [23] presented a general framework for $T_{\mathcal{M}}$ for nonnegative matrices to unify these threshold parameters. However, the definition of $T_{\mathcal{M}}$ in [23, 32] is limited to non-negative matrices of finite dimension. Motivated by these two works, in this paper we propose to introduce a general definition of target reproduction number for positive operators on an ordered Banach space of infinite dimension. It is worth pointing out that unlike the basic reproduction number and the type reproduction number, the target reproduction number, in general, doesn't correspond to population renewal dynamics of specific host types.

The remainder of the paper is organized as follows. In Section 2, we briefly summarize the theory of basic reproduction numbers R_0 for reaction-diffusion models. In Section 3, we establish the theory of target reproduction numbers $T_{\mathcal{M}}$ for positive operators on an ordered Banach space, and then apply it to reaction-diffusion population models by choosing a specific class of target operators, denoted as T_S, for which we prove that $\text{sign}(R_0 - 1) = \text{sign}(T_S - 1)$, and T_S can be viewed as R_0 of a modified system. We also give a characterization of T_S so that it can be easily computed numerically. In Section 4, we use two examples of reaction-diffusion population models to illustrate our analytic results.

2 Basic reproduction number R_0

In this section, we briefly summarize the theory of basic reproduction numbers for reaction-diffusion population models.

Let Ω be a bounded spatial domain with smooth boundary $\partial\Omega$. We consider a linear reaction-diffusion system

$$\begin{aligned} &\frac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) + F(x)u - V(x)u, && t > 0,\ x \in \Omega, \\ &\Gamma u = 0, && t > 0,\ x \in \partial\Omega, \end{aligned} \tag{1}$$

where $\nabla \cdot (d(x)\nabla u) = \text{diag}(\nabla \cdot (d_1(x)\nabla u_1), \cdots, \nabla \cdot (d_m(x)\nabla u_m))$ and $\Gamma u = (\Gamma_1 u_1, \cdots, \Gamma_m u_m)$ denotes the boundary condition. Assume that $d_i \in C^1(\Omega)$ and either $d_i(x) > 0, \forall x \in \bar{\Omega}$, or $d_i(x) \equiv 0$ on $\bar{\Omega}$, for each $1 \le i \le m$. In the case where $d_i(x) \equiv 0$, we do not impose any boundary condition on u_i. For simplicity of our presentation, we choose $\Gamma_i u_i$ to be the Robin type boundary condition in the case where $d_i(x) > 0, \forall x \in \bar{\Omega}$. However, the theory of R_0 can be developed for the case of the Dirichlet boundary condition in a similar manner.

Let $X = C(\bar{\Omega}, \mathbb{R}^m)$ and $X^+ = C(\bar{\Omega}, \mathbb{R}^m_+)$. Then (X, X^+) is an ordered Banach space with the positive cone X^+ having nonempty interior. For a linear operator $\mathcal{L}$, let $\sigma(\mathcal{L})$ denote its spectrum set, and its spectral bound is defined as $s(\mathcal{L}) := \sup\{\text{Re}(\lambda) : \lambda \in \sigma(\mathcal{L})\}$.

Recall that a matrix is said to be cooperative if all of its offdiagonal elements are nonnegative. Following the setting in [38] (see also [40, Section 11.3]), we assume that

(H1) $F(x)$ is a continuous and nonnegative $m \times m$ matrix function on $\bar{\Omega}$.
(H2) $-V(x)$ is a continuous and cooperative $m \times m$ matrix function on $\bar{\Omega}$, and $s(\nabla \cdot (d(x)\nabla) - V) < 0$.

Define $L : X \to X$ by

$$[L(\phi)](x) = F(x) \int_0^\infty [T(t)\phi](x)dt, \quad \forall\, \phi \in X,\ x \in \Omega,$$

where $T(t)$ is the solution semigroup on X of the following linear system

$$\begin{array}{ll} \dfrac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) - V(x)u, & t > 0,\ x \in \Omega, \\ \Gamma u = 0, & t > 0,\ x \in \partial\Omega. \end{array}$$

Then the basic reproduction number (ratio) for system (1) is defined as $R_0 = r(L)$, the spectral radius of L.

Theorem 1 ([38, THEOREM 3.1]) *$R_0 - 1$ has the same sign as $s(B + F)$, where $B = \nabla \cdot (d(x)\nabla) - V$.*

Theorem 2 ([38, THEOREM 3.2]) *Assume that $d_i(x) > 0$, $\forall x \in \bar{\Omega}$, for all $1 \le i \le m$. If the elliptic eigenvalue problem*

$$\begin{array}{ll} -\nabla \cdot (d(x)\nabla\phi) + V(x)\phi = \mu F(x)\phi, & x \in \Omega \\ \Gamma u = 0, & x \in \partial\Omega \end{array}$$

admits a unique positive eigenvalue μ_0 with a positive eigenfunction, then $R_0 = \dfrac{1}{\mu_0}$.

Consider the linear reaction-diffusion system with parameter $\lambda > 0$:

$$\begin{array}{ll} \dfrac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) + \dfrac{1}{\lambda}F(x)u - V(x)u, & t > 0,\ x \in \Omega, \\ \Gamma u = 0, & t > 0,\ x \in \partial\Omega. \end{array} \tag{2}$$

Let $Q_\lambda(t)$ be the solution semigroup generated by system (2) on X; that is, $Q_\lambda(t)\phi = u(t, \cdot, \phi)$, where $u(t, x, \phi)$ is the unique solution of system (2) with $u(0, \cdot, \phi) = \phi \in X$.

Theorem 3 *If $R_0 > 0$, then $\lambda = R_0$ is the unique solution of $s\left(B + \frac{1}{\lambda}F\right) = 0$, and is also the unique solution of $r(Q_\lambda(t_0)) = 1$ for any given $t_0 > 0$.*

Proof Let $R(\lambda)$ be the basic reproduction number of system (2). It is easy to see that $R(\lambda) = \dfrac{1}{\lambda}R_0,\ \forall\lambda > 0$. This implies that $R(R_0) = 1$; $R(\lambda) < 1, \forall\lambda > R_0$; and $R(\lambda) > 1, \forall\lambda < R_0$. By Theorem 1, as applied to system (2), it then follows that $s\left(B + \frac{1}{R_0}F\right) = 0$; $s\left(B + \frac{1}{\lambda}F\right) < 0$, $\forall\lambda > R_0$; and $s\left(B + \frac{1}{\lambda}F\right) > 0$, $\forall\lambda < R_0$. Thus, $\lambda = R_0$ is the unique solution of $s\left(B + \frac{1}{\lambda}F\right) = 0$.

Let $\omega(Q_\lambda)$ be the exponential growth bound of the semigroup $Q_\lambda(t)$ (see, e.g., definition (3.3) in [33]). In view of formula (3.4) in [33], we have $\omega(Q_\lambda) =$

$\frac{\ln r(Q_\lambda(t_0))}{t_0}$, $\forall t_0 > 0$. Further, [33, Theorem 3.14 (iv)] gives rise to $\omega(Q_\lambda) = s(B + \frac{1}{\lambda}F)$. It then follows that $r(Q_\lambda(t_0)) = e^{s(B+\frac{1}{\lambda}F)t_0}$ for any given $t_0 > 0$. This observation, together with the first statement, implies the desired second statement. □

For a given continuous $m \times m$ matrix function $M(x)$, we define a linear operator $\tilde{M} : X \to X$ by

$$[\tilde{M}\phi](x) = M(x)\phi(x), \quad \forall\, x \in \bar{\Omega},\ \phi \in X. \tag{3}$$

By [33, Theorem 3.12], it follows that

$$(\lambda I - B)^{-1}\phi = \int_0^\infty e^{-\lambda t}T(t)\phi dt, \quad \forall \lambda > s(B),\ \phi \in X.$$

In particular, since $s(B) < 0$, we have

$$-B^{-1}\phi = \int_0^\infty T(t)\phi dt,$$

and hence,

$$L = -\tilde{F}B^{-1}. \tag{4}$$

Remark 1 If we replace the diffusion term in system (1) with the general uniformly elliptic operator of second order and impose the Dirichlet boundary conditions or a mixture of Dirichlet and Robin type boundary conditions, then all the results in Section 2 are still valid. Further, in the case where $\Omega = \mathbb{R}$, all the results in Section 2 also hold true provided that we replace the diffusion term in system (1) with a spatially periodic and uniformly elliptic operator of second order and impose the periodic boundary conditions.

3 Target reproduction number $T_{\mathcal{M}}$

In this section, we first introduce a general definition of target reproduction numbers $T_{\mathcal{M}}$ for positive operators on an ordered Banach space, and then apply it to reaction-diffusion models by choosing a specific class of target operators.

3.1 A general definition

Let (E, P) be an ordered Banach space with the positive cone P. For $x, y \in E$, we write $x \leq y$ if $y - x \in P$. We first recall some basic concepts.

Definition 1 A linear operator M on E is said to be positive if $M(P) \subset P$. For two linear operators M_1 and M_2 on E, we write $M_1 \leq M_2$ provided that $M_2 - M_1$ is a positive operator.

Definition 2 A closed linear operator M on E is said to be resolvent-positive if its resolvent set, $\rho(M) := \{\lambda \in \mathbb{C} : \lambda I - M$ has a bounded inverse operator that is defined on $E\}$, contains (ω, ∞) and $\lambda I - M$ is a positive operator for all $\lambda > \omega$.

Definition 3 The cone P is said to be normal if there exists a positive constant C such that $\|x\| \leq C\|y\|$ whenever $0 \leq x \leq y$; and the cone P is said to be generating (reproducing) if $E = P - P$.

Throughout this section, we assume that $E \neq \{0\}$ and P is normal and generating (reproducing). To develop a general theory of target reproduction numbers, we need the following two preliminary results.

Lemma 4 ([33, THEOREM 3.5]) *Let $\mathcal{B}$ be a resolvent-positive operator on E with $s(\mathcal{B}) < 0$, and $\mathcal{A} = \mathcal{B} + \mathcal{C}$ be a positive perturbation of $\mathcal{B}$. If $\mathcal{A}$ is resolvent-positive, then $s(\mathcal{A})$ has the same sign as $r(-\mathcal{C}\mathcal{B}^{-1}) - 1$.*

Lemma 5 ([33, THEOREM 3.10]) *Let $Q, C : E \to E$ be positive linear operators with $r(Q) < 1$. Then $r(Q+C)-1$ has the same sign as $r(C(I-Q)^{-1})-1$.*

Let $\mathcal{L}$ and $\mathcal{M}$ be two positive operators on E such that $\mathcal{M} \leq \mathcal{L}$. We choose $\mathcal{M}$ as the target operator. Clearly, the operator $\mathcal{N} := \mathcal{L} - \mathcal{M}$ is positive. We further assume that

(H3) $r(\mathcal{N}) < 1$.

Then we can define a linear operator $\mathcal{L}_T$ on E by

$$\begin{aligned}\mathcal{L}_T &= \mathcal{M} + \mathcal{M}\mathcal{N} + \mathcal{M}\mathcal{N}^2 + \cdots + \mathcal{M}\mathcal{N}^n + \cdots \\ &= \mathcal{M}(I - \mathcal{N})^{-1},\end{aligned}$$

where I is the identity operator on E. Motivated by [23], we introduce the following definition.

Definition 4 The target reproduction number is defined as the spectral radius of $\mathcal{L}_T$; that is,

$$T_{\mathcal{M}} = r(\mathcal{L}_T) = r\big(\mathcal{M}(I - \mathcal{N})^{-1}\big).$$

In the case where $\mathcal{L}$ is the next generation operator, if we choose the target operator $\mathcal{M} = \mathcal{L}$, then $\mathcal{N}$ is the zero operator on E, and hence, $T_{\mathcal{M}} = r(\mathcal{L}) = R_0$. Thus, R_0 can be regarded as the target reproduction number when the control is targeted at the entire set of the population.

Since $\mathcal{L} = \mathcal{N} + \mathcal{M}$ and $r(\mathcal{N}) < 1$, as a straightforward consequence of Lemma 5, we have the following result.

Theorem 6 *$sign(r(\mathcal{L}) - 1) = sign(T_{\mathcal{M}} - 1)$, and hence, $r(\mathcal{L}) = 1$, $r(\mathcal{L}) < 1$,and $r(\mathcal{L}) > 1$ are equivalent to $T_{\mathcal{M}} = 1$, $T_{\mathcal{M}} < 1$, and $T_{\mathcal{M}} > 1$, respectively.*

Define a family of positive linear operators with parameter $\lambda > 0$:

$$\mathcal{P}(\lambda) = \frac{\mathcal{M}}{\lambda} + \mathcal{N}, \ \forall\ \lambda > 0. \tag{5}$$

Theorem 7 *If $T_{\mathcal{M}} > 0$, then $\lambda = T_{\mathcal{M}}$ is the unique positive solution of $r(\mathcal{P}(\lambda)) = 1$.*

Proof Let $T(\lambda)$ be the target reproduction number of $\mathcal{P}(\lambda)$ associated with the target operator $\dfrac{\mathcal{M}}{\lambda}$. Clearly, we have

$$T(\lambda) = r\left(\frac{1}{\lambda}\mathcal{M}(I-\mathcal{N})^{-1}\right) = \frac{1}{\lambda}T_{\mathcal{M}},\ \forall\ \lambda > 0.$$

Note that $T(T_{\mathcal{M}}) = 1; T(\lambda) < 1, \forall\ \lambda > T_{\mathcal{M}}; T(\lambda) > 1, \forall\ \lambda < T_{\mathcal{M}}$. By Theorem 6, it then follows that

$$r(\mathcal{P}(\lambda)) = 1\ (<1, >1) \text{ if and only if } \lambda = T_{\mathcal{M}}\ (> T_{\mathcal{M}}, < T_{\mathcal{M}}).$$

This implies that $\lambda = T_{\mathcal{M}}$ is the unique positive solution of $r(\mathcal{P}(\lambda)) = 1$. □

It is easy to see that $\mathcal{P}(\lambda) = \mathcal{L} - (1 - 1/\lambda)\mathcal{M}$. In the case where $T_{\mathcal{M}} > 1$, Theorem 7 implies that $r(\mathcal{P}(T_{\mathcal{M}})) = 1$. Thus, the change required for the target operator $\mathcal{M}$ to ensure that the disease/population fertility is controlled is quantified by the proportion $1 - 1/T_{\mathcal{M}}$. Biologically, this indicates that the target reproduction number, $T_{\mathcal{M}}$, measures the strength of control needed when targeting a specific set.

Remark 2 Theorems 6 and 7 are extensions of [23, Theorems 2 and 1], respectively, to positive operators on an ordered Banach space of infinite dimension. With [27, Theorem 4.3], one can easily obtain an analog of [23, Theorem 3].

Remark 3 For integro-difference population models with spatial structure (see, e.g., [25] and references therein), by a linearization procedure, we may obtain a linear discrete-time system

$$u_{n+1}(x) = [\mathcal{L}u_n](x) := [\mathcal{M}u_n](x) + [\mathcal{N}u_n](x), \quad \forall x \in \Omega,\ n \geq 0,$$

where $\mathcal{M}$ is the new production (or infection) operator, and $\mathcal{N}$ is the transition operator. As such, $T_{\mathcal{M}}$ is the traditional basic reproduction number. Consequently, Theorems 6 and 7 can be employed to study the evolution dynamics and compute R_0 for those integro-difference models.

3.2 A class of $T_{\mathcal{M}}$ for reaction-diffusion systems

In this subsection, we introduce a class of target reproduction numbers for reaction-diffusion population models with compartmental structure, where the target is focused on new infection or production.

Let $N_m = \{1, 2\cdots, m\}$ and $S \subset N_m \times N_m$ be a given target set. For any continuous $m \times m$ matrix function $M(x)$, define $M_S(x) = (M_S^{ij}(x))_{m\times m}$ by

$$M_S^{ij}(x) = \begin{cases} M_{ij}(x), & \text{if } (i,j) \in S, \\ 0, & \text{otherwise.} \end{cases}$$

Let $F(x)$, $V(x)$ and B be defined as in Section 2, and define two linear operators:

$$\mathcal{M} = -\tilde{F}_S B^{-1}, \quad \mathcal{N} = -(\tilde{F} - \tilde{F}_S)B^{-1}. \tag{6}$$

We choose $\mathcal{M}$ to be the target operator for $\mathcal{L} := -\tilde{F}B^{-1} = \mathcal{M} + \mathcal{N}$. In this case, (H3) reduces to

(H3′) $r(-(\tilde{F} - \tilde{F}_S)B^{-1}) < 1$.

According to Definition 4, the corresponding target reproduction number is

$$T_S = r\big(\mathcal{M}(I - \mathcal{N})^{-1}\big) = r\left(-\tilde{F}_S B^{-1}\left(I + (\tilde{F} - \tilde{F}_S)B^{-1}\right)^{-1}\right).$$

Note that if $S = \{i_1, i_2, \cdots, i_l\} \times N_m$, then T_S denotes the type $(i_1, i_2, \cdots, i_l)$ reproduction number (see [17]). Particularly, if $S = \{i\} \times N_m$, then we use T_i to denote T_S for simplicity. To compare with the definition of T_S for nonnegative matrices in [32], we need an elementary result on matrices.

Lemma 8 *Let M and W be two $m \times m$ constant matrices. Then the following statements hold true:*

(i) If $S = H \times N_m$ with $H \subset N_m$, then $(MW)_S = M_S W$.
(ii) If W is diagonal, then $(MW)_S = M_S W$ for any $S \subset N_m \times N_m$.

Proof (i) Define $E_H = \mathrm{diag}(a_1, a_2, \cdots, a_m)$, where $a_l = 1$ if $l \in H$ and $a_l = 0$ if $l \notin H$. For any $m \times m$ matrix K, we have

$$(E_H K)_{ij} = \sum_{h=1}^{m} (E_H)_{ih} K_{hj} = (E_H)_{ii} K_{ij} = \begin{cases} K_{ij}, & \text{if } i \in H, \\ 0, & \text{otherwise,} \end{cases}$$

and hence, $E_H K = K_S$. It then follows that $(MW)_S = E_H(MW) = (E_H M)W = M_S W$.

(ii) Note that $(MW)_{ij} = \sum_{h=1}^{m} M_{ih} W_{hj}$, and $(M_S W)_{ij} = \sum_{h=1}^{m} (M_S)_{ih} W_{hj}$, $\forall 1 \le i, j \le m$. In the case where W is diagonal, we have $(MW)_{ij} = M_{ij} W_{jj}$, $\forall 1 \le i, j \le m$, and

$$(M_S W)_{ij} = (M_S)_{ij} W_{jj} = \begin{cases} M_{ij} W_{jj}, & \text{if } (i,j) \in S, \\ 0, & \text{otherwise.} \end{cases}$$

This shows that $(MW)_S = M_S W$. □

Returning to the compartmental ODE model, we let $d_i(x) \equiv 0$, $F(x) \equiv F$ and $V(x) \equiv V$. It then follows that $B = -V$, and hence, $\mathcal{L} = FV^{-1}$ is the next generation matrix. Choose $\mathcal{M} = F_S V^{-1}$ and $\mathcal{N} = FV^{-1} - F_S V^{-1}$. In the case where $S = H \times N_m$ with $H \subset N_m$, Lemma 8 (i) implies that $F_S V^{-1} = (FV^{-1})_S$, and hence, our definition of T_S agrees with the type reproduction number defined in [12,28,32]. For a general target set $S \subset N_m \times N_m$, it follows from Lemma 8 (ii) that $F_S V^{-1} = (FV^{-1})_S$ if the matrix V is diagonal. Thus, our definition of T_S is also consistent with the target reproduction number defined in [32] in the case where V is diagonal.

The subsequent result follows directly from Theorem 6.

Theorem 9 *Let* (H1), (H2) *and* (H3′) *hold. Then* $R_0 - 1$ *has the same sign as* $T_S - 1$.

Theorem 10 *Let* (H1), (H2) *and* (H3′) *hold. Then* $s(B + (\tilde{F} - \tilde{F}_S)) < 0$ *and* $\mathcal{L}_T = -\tilde{F}_S\big(B + (\tilde{F} - \tilde{F}_S)\big)^{-1}$.

Proof Note that B is a resolvent-positive operator on X with $s(B) < 0$ by (H2). Clearly, $\tilde{F} - \tilde{F}_S$ is a positive operator on X, and $B + (\tilde{F} - \tilde{F}_S)$ is resolvent-positive. By Lemma 4 with $\mathcal{B} = B$ and $\mathcal{C} = \tilde{F} - \tilde{F}_S$, it follows that $s(B + (\tilde{F} - \tilde{F}_S))$ has the same sign as $r(-(\tilde{F} - \tilde{F}_S)B^{-1}) - 1 = r(\mathcal{N}) - 1$. Since $r(\mathcal{N}) < 1$, we obtain $s(B + (\tilde{F} - \tilde{F}_S)) < 0$.

Since $s(B + (\tilde{F} - \tilde{F}_S)) < 0$ and $B + (\tilde{F} - \tilde{F}_S)$ is resolvent-positive, $\big(B + (\tilde{F} - \tilde{F}_S)\big)^{-1}$ exists (see [33, Theorem 3.12]). It then follows that

$$\begin{aligned}
\mathcal{L}_T &= \mathcal{M}(I - \mathcal{N})^{-1} \\
&= \mathcal{M}(I - (\mathcal{L} - \mathcal{M}))^{-1} \\
&= \mathcal{M}\Big(I - (-\tilde{F}B^{-1} + \tilde{F}_S B^{-1})\Big)^{-1} \\
&= -\tilde{F}_S B^{-1}\Big(I + \tilde{F}B^{-1} - \tilde{F}_S B^{-1})\Big)^{-1} \\
&= -\tilde{F}_S B^{-1}\Big(I + (\tilde{F} - \tilde{F}_S)B^{-1})\Big)^{-1} \\
&= -\tilde{F}_S\Big(\big(I + (\tilde{F} - \tilde{F}_S)B^{-1})\big)B\Big)^{-1} \\
&= -\tilde{F}_S\Big(B + (\tilde{F} - \tilde{F}_S)\Big)^{-1}.
\end{aligned}$$

This completes the proof. □

Remark 4 By virtue of (4), $-\tilde{F}_S\Big(B + (\tilde{F} - \tilde{F}_S)\Big)^{-1}$ is the next generation operator of linear system (1) with $F(x)$ and $V(x)$ replaced by $F_S(x)$ and $V(x) - (F(x) - F_S(x))$, respectively. Thus, Theorem 10 implies that

$$T_S = r(\mathcal{L}_T) = r\Big(-\tilde{F}_S\big(B + (\tilde{F} - \tilde{F}_S)\big)^{-1}\Big)$$

is the basic reproduction number of such a modified system.

In the case where $S = \{(i, j)\}$, we use T_{ij} to denote T_S for simplicity. We then have the following observation.

Theorem 11 *Let* k_1 *and* k_2 *be two integers such that* $k_1 + k_2 = m$, *and define* $S_1 := \{1, \cdots, k_1\} \times \{k_1 + 1, \cdots, m\}$, $S_2 := \{k_1 + 1, \cdots, m\} \times \{1, \cdots, k_1\}$. *Assume that* (H1), (H2) *and* (H3′) *hold for* $S = S_1$ *and* $S = S_2$, *and the* $m \times m$ *matrix* $V(x)$ *can be written as*

$$V(x) = \begin{pmatrix} V_{11}(x) & 0 \\ 0 & V_{22}(x) \end{pmatrix},$$

where $V_{ii}(x)$ *is a* $k_i \times k_i$ *matrix for* $i = 1, 2$. *Then* $T_{S_1} = T_{S_2}$. *Particularly, if* $m = 2$ *and* $V(x) = diag(V_{11}(x), V_{22}(x))$, *then* $T_{12} = T_{21}$.

Proof Let $X_i = C(\bar{\Omega}, \mathbb{R}^{k_i})$ for $i = 1, 2$. Clearly, $X = X_1 \times X_2$. For a given $\Phi = (\Phi_{k_1}, \Phi_{k_2}) \in X$, we use the following notations:

$$\begin{aligned}
&\Phi_{k_1} = (\phi_1, \phi_2, \cdots, \phi_{k_1}), \quad \Phi_{k_2} = (\phi_{k_1+1}, \phi_{k_1+2}, \cdots, \phi_m),\\
&\nabla \cdot \big(D_{k_1}(x)\nabla\Phi_{k_1}\big) = \mathrm{diag}\Big(\nabla \cdot \big(d_1(x)\nabla\phi_1\big), \cdots, \nabla \cdot \big(d_{k_1}(x)\nabla\phi_{k_1}\big)\Big),\\
&\nabla \cdot \big(D_{k_2}(x)\nabla\Phi_{k_2}\big) = \mathrm{diag}\Big(\nabla \cdot \big(d_{k_1+1}(x)\nabla\phi_{k_1+1}\big), \cdots, \nabla \cdot \big(d_m(x)\nabla\phi_m\big)\Big).
\end{aligned}$$

Let $L_{S_i} := -\tilde{F}_{S_i}\Big(B + (\tilde{F} - \tilde{F}_{S_i})\Big)^{-1}$ for $i = 1, 2$. Then Theorem 10 implies that $T_{S_i} = r(L_{S_i})$ for $i = 1, 2$. We write the $m \times m$ matrix $F(x)$ as

$$F(x) = \begin{pmatrix} F_{11}(x) & F_{12}(x) \\ F_{21}(x) & F_{22}(x) \end{pmatrix},$$

where $F_{ii}(x)$ is a $k_i \times k_i$ matrix for $i = 1, 2$. It then follows that

$$F_{S_1}(x) = \begin{pmatrix} 0 & F_{12}(x) \\ 0 & 0 \end{pmatrix}, \quad F(x) - F_{S_1}(x) = \begin{pmatrix} F_{11}(x) & 0 \\ F_{21}(x) & F_{22}(x) \end{pmatrix}.$$

It is easy to see that $L_{S_1}(X_1 \times X_2) \subset X_1 \times \{0\}$. Let $L_{S_1}|_{X_1\times\{0\}}$ be the restriction of L_{S_1} onto $X_1 \times \{0\}$. Since $X_1 \times \{0\}$ is a subspace of X, we have $r(L_{S_1}) = r\left(L_{S_1}|_{X_1\times\{0\}}\right)$. For any $(\Phi_{k_1}, 0) \in X_1 \times \{0\}$, let

$$\Big(B + (\tilde{F} - \tilde{F}_{S_1})\Big)^{-1} \begin{pmatrix} \Phi_{k_1} \\ 0 \end{pmatrix} = \begin{pmatrix} \Psi_{k_1} \\ \Psi_{k_2} \end{pmatrix}, \quad \text{where } \Psi_{k_i} \in X_i,\ i = 1, 2.$$

It then follows that

$$\Big(B + (\tilde{F} - \tilde{F}_{S_1})\Big) \begin{pmatrix} \Psi_{k_1} \\ \Psi_{k_2} \end{pmatrix} = \begin{pmatrix} \Phi_{k_1} \\ 0 \end{pmatrix},$$

and hence,

$$\begin{aligned}
&\nabla \cdot (D_{k_1}(x)\nabla\Psi_{k_1}(x)) - V_{11}(x)\Psi_{k_1}(x) + F_{11}(x)\Psi_{k_1}(x) = \Phi_{k_1}(x), && x \in \Omega,\\
&\nabla \cdot (D_{k_2}(x)\nabla\Psi_{k_2}(x)) - V_{22}(x)\Psi_{k_2}(x) + F_{21}(x)\Psi_{k_1}(x) + F_{22}(x)\Psi_{k_2}(x) = 0, && x \in \Omega.
\end{aligned}$$

Letting $B_i = \nabla \cdot (D_{k_i}(x)\nabla) - \tilde{V}_{ii} + \tilde{F}_{ii}$ for $i = 1, 2$, we then obtain

$$\begin{aligned}
&B_1\Psi_{k_1}(x) = \Phi_{k_1}(x),\ x \in \Omega,\\
&B_2\Psi_{k_2}(x) = -F_{21}(x)\Psi_{k_1}(x),\ x \in \Omega.
\end{aligned}$$

Since

$$\begin{pmatrix} B_1 & 0 \\ 0 & B_2 \end{pmatrix} \le B + \tilde{F} - \tilde{F}_{S_1},$$

we see from Theorem 10 that

$$s\left(\begin{pmatrix} B_1 & 0 \\ 0 & B_2 \end{pmatrix}\right) \le s\big(B + \tilde{F} - \tilde{F}_{S_1}\big) < 0.$$

This implies that $s(B_i) < 0$, $i = 1, 2$, and hence, B_i^{-1} exists for each $i = 1, 2$. It then follows that

$$\begin{aligned}\Psi_{k_1} &= B_1^{-1}\Phi_{k_1},\\ \Psi_{k_2} &= -B_2^{-1}\tilde{F}_{21}\Psi_{k_1} = -B_2^{-1}\tilde{F}_{21}B_1^{-1}\Phi_{k_1}.\end{aligned}$$

Thus,

$$L_{S_1}\begin{pmatrix}\Phi_{k_1}\\ 0\end{pmatrix} = \begin{pmatrix}-\tilde{F}_{12}\Psi_{k_2}\\ 0\end{pmatrix} = \begin{pmatrix}\tilde{F}_{12}B_2^{-1}\tilde{F}_{21}B_1^{-1}\Phi_{k_1}\\ 0\end{pmatrix}.$$

Letting $L_1 = \tilde{F}_{12}B_2^{-1}\tilde{F}_{21}B_1^{-1}$ on X_1, we then obtain

$$T_{S_1} = r(L_{S_1}) = r\left(L_{S_1}|_{X_1\times\{0\}}\right) = r(L_1).$$

Similarly, for the target set S_2, we have

$$T_{S_2} = r(L_{S_2}) = r\left(L_{S_2}|_{\{0\}\times X_2}\right) = r(L_2),$$

where $L_2 = \tilde{F}_{21}B_1^{-1}\tilde{F}_{12}B_2^{-1}$ on X_2. Let $A_2 = \tilde{F}_{12}B_2^{-1}$ and $A_1 = \tilde{F}_{21}B_1^{-1}$. Then

$$L_1 = A_2A_1, \quad L_2 = A_1A_2.$$

Clearly, $A_1 : X_1 \to X_2$ and $A_2 : X_2 \to X_1$ are two bounded linear operators. By the formula of the spectral radius, it then follows that

$$r(L_1) = r(L_2)$$

and hence, $T_{S_1} = T_{S_2}$. □

We remark that the results similar to Theorem 11 were established in [32, Theorems 4.1 and 4.2] for nonnegative matrices under the assumption that the next generation matrix K is irreducible and the weighted digraph associated with K is weight balanced.

The subsequent two results follows from Theorems 2 and 3 and Remark 4.

Theorem 12 *Assume that $d_i(x) > 0$, $\forall\, x \in \bar{\Omega}$, $1 \le i \le m$. If the elliptic eigenvalue problem*

$$\begin{aligned}&-\nabla\cdot(d(x)\nabla\phi) + \Big(V(x) - \big(F(x) - F_S(x)\big)\Big)\phi = \mu F_S(x)\phi, && x \in \Omega,\\ &\Gamma\phi = 0, && x \in \partial\Omega,\end{aligned} \tag{7}$$

admits a unique positive eigenvalue μ_0 with a positive eigenfunction, then $T_S = \dfrac{1}{\mu_0}$.

Theorem 13 *If $T_S > 0$, then $\lambda = T_S$ is the unique solution of $r(\Phi_\lambda(t_0)) = 1$ for any given $t_0 > 0$, where $\Phi_\lambda(t)$ is the solution semigroup of the following linear reaction-diffusion system with parameter $\lambda > 0$:*

$$\begin{aligned}\tfrac{\partial u}{\partial t} =\ & \nabla\cdot(d(x)\nabla u) - V(x)u + \tfrac{1}{\lambda}F_S(x)u\\ & +(F(x) - F_S(x))u, && x \in \Omega,\ t > 0,\\ \Gamma\phi =\ & 0, && x \in \partial\Omega,\ t > 0.\end{aligned} \tag{8}$$

It is worth pointing out that Theorem 13 is also a straightforward consequence of Theorem 7. Indeed, substituting (6) into (5), we have

$$\begin{aligned}\mathcal{P}(\lambda) &= \frac{1}{\lambda}\mathcal{M}+\mathcal{N}\\ &= \frac{1}{\lambda}\left(-\tilde{F}_S B^{-1}\right)-(\tilde{F}-\tilde{F}_S)B^{-1}\\ &= -\left(\frac{1}{\lambda}\tilde{F}_S+\tilde{F}-\tilde{F}_S\right)B^{-1}.\end{aligned}$$

Thus, $\mathcal{P}(\lambda)$ is the next generation operator of the linear reaction-diffusion system (8). It follows from Theorem 7 that $\lambda = T_S$ is the unique solution of $r(\mathcal{P}(\lambda)) = 1$, and hence, $s\left(\nabla\cdot(d(x)\nabla)-\big(V-(F-F_S)\big)+\frac{1}{T_S}F_S\right)=0$. This implies the desired conclusion in Theorem 13 (see the proof of Theorem 3).

Remark 5 In view of Theorem 13, we can use [24, Lemma 2.5], combined with the bisection method, to solve $r(\Phi_\lambda(t_0)) = 1$ numerically for any given $t_0 > 0$ (e.g., letting $t_0 = 1$), and then obtain the approximate value of T_S. An alternative way to compute T_S is to solve the eigenvalue problem (7) numerically, and then $T_S = \frac{1}{\mu_0}$ according to Theorem 12.

Note that we write the coefficient matrix in the reaction term of linear system (1) as $J = F - V$. In epidemiology, F is the transmission matrix which captures the new infections, and V is the transfer matrix which captures the transitions. As discussed in [23], the biological interpretations of F and V may be subtle due to the complexity of biological problems. This in turn leads to a different decomposition of J and hence, a different expression of the basic reproduction numbers (see, e.g., [4,30]). In order to generalize [23, Theorem 6] to reaction-diffusion models, we assume that $F_1(x)-V_1(x) = F_2(x)-V_2(x)$ and each pair of F_i and V_i satisfies (H1) and (H2). Letting $B_i := \nabla\cdot(d(x)\nabla)-\widetilde{V}_i$, we then obtain two basic reproduction numbers:

$$R_0^{(i)} = r(-\widetilde{F}_i B_i^{-1}),\quad i = 1,2.$$

Theorem 14 *Assume that* $F_1(x) \geq F_2(x),\ \forall x\in\Omega$, *and* $r\left(-(\widetilde{F_1}-\widetilde{F_2})B_1^{-1}\right) < 1$. *Then* $R_0^{(2)}$ *is the target reproduction number for* $\mathcal{L} = -\widetilde{F_1}B_1^{-1}$ *corresponding to the target operator* $\mathcal{M} = -\widetilde{F_2}B_1^{-1}$.

Proof Clearly, $\mathcal{M}$ is a positive linear operator. Since $F_1(x)\geq F_2(x)$, $\forall x\in\Omega$, it follows that $\mathcal{N} := \mathcal{L}-\mathcal{M} = -\left(\widetilde{F_1}-\widetilde{F_2}\right)B_1^{-1}$ is also positive. In view of $\widetilde{F_1}-\widetilde{F_2} = \widetilde{V_1}-\widetilde{V_2}$, we have

$$\begin{aligned}\mathcal{M}(I-\mathcal{N})^{-1} &= -\widetilde{F_2}B_1^{-1}\left[I+\left(\widetilde{F_1}-\widetilde{F_2}\right)B_1^{-1}\right]^{-1}\\ &= -\widetilde{F_2}\left[B_1+\left(\widetilde{F_1}-\widetilde{F_2}\right)\right]^{-1}\\ &= -\widetilde{F_2}\left[B_1+\left(\widetilde{V_1}-\widetilde{V_2}\right)\right]^{-1}\\ &= -\widetilde{F_2}B_2^{-1}.\end{aligned}$$

Thus, $T_{\mathcal{M}} = r\left(\mathcal{M}(I-\mathcal{N})^{-1}\right) = r\left(-\widetilde{F_2}B_2^{-1}\right) = R_0^{(2)}$. □

Remark 6 If the diffusion term and boundary conditions of system (1) are changed in the same way as in Remark 1, then all results in section 3 still hold true.

4 Applications

In this section, we apply the developed theory of target reproduction numbers to two reaction-diffusion population models.

4.1 An epidemic model of cholera

Cholera is an acute intestinal infectious disease caused by the bacterium *Vibrio cholerae*. It can spread rapidly and lead to death within days if left untreated. The complexity of cholera dynamics stems from the fact that both direct (i.e., human-to-human) and indirect (i.e., environment-to-human) routes are involved in the disease transmission.

A reaction-convection-diffusion model was proposed in [39], which is based on a SIRS-P (susceptible-infected-recovered-susceptible-pathogen) compartment structure. This model incorporates the spatial movement of human hosts and pathogens, and the periodic contact and growth rates to take into account the seasonality of the disease transmission. We consider a special case of this model with parameters independent of time:

$$\begin{aligned}
\frac{\partial S}{\partial t} &= \Lambda - S\beta_1(x)I - S\beta_2(x)\frac{P}{P+K} - d\,S + \sigma R + D_1\frac{\partial^2 S}{\partial x^2},\\
\frac{\partial I}{\partial t} &= S\beta_1(x)I + S\beta_2(x)\frac{P}{P+K} - (d+\gamma)I + D_2\frac{\partial^2 I}{\partial x^2},\\
\frac{\partial R}{\partial t} &= \gamma I - (d+\sigma)R + D_3\frac{\partial^2 R}{\partial x^2},\\
\frac{\partial P}{\partial t} &= \xi(x)I + g(x)P\left(1-\frac{P}{K_P}\right) - \delta P - \nu\frac{\partial P}{\partial x} + D_4\frac{\partial^2 P}{\partial x^2},
\end{aligned} \tag{9}$$

for $x \in [0,1]$ and $t > 0$, with no flux boundary condition

$$\begin{aligned}
&\frac{\partial U}{\partial x}(0,t) = \frac{\partial U}{\partial x}(1,t) = 0, \quad U = S, I, R\,, t > 0,\\
&D_4\frac{\partial P}{\partial x}(x,t) - \nu P(x,t) = 0, \quad x = 0,\, 1, \quad t > 0,
\end{aligned} \tag{10}$$

and the initial condition

$$U(x,0) = U_0(x) \geq 0, \quad U = S, I, R, P, \quad 0 \leq x \leq 1. \tag{11}$$

Here $t \geq 0$ is the time variable, $x \in [0,1]$ is the location variable, and $x = 0$ and 1 represent two ends of the theoretical river. $S = S(x,t), I = I(x,t)$,

and $R = R(x,t)$ measure the densities of susceptible, infectious, and recovered human hosts at location x and time t, respectively. $P = P(x,t)$ denotes the concentration of cholera in the water environment. The parameter D_i $(1 \le i \le 4)$ is the diffusion coefficient of S, I, R and P, respectively, and v is the advection coefficient depicting the drift for vibrio's transport. The definition and value of the other parameters provided in Table 1, where the base parameter values are mainly taken from [39]. In the numerical simulations for the target reproduction numbers, we assume that $D_2 = D_4 = \nu = 1$.

Table 1 Definition of parameters of cholera model (9) (note that p, y, w and d denote a person, year, week and day, respectively.)

	Definition	Base value
Λ	Recruitment rate of susceptible hosts	$0.7914\,\mathrm{p\,d^{-1}}$
d	Natural death rate of human	$(43.5 \times 365\,\mathrm{d})^{-1}$
β_1	Direct transmission rate	$1.5714 \times 10^{-5}\ \mathrm{p^{-1}d^{-1}}$
β_2	Indirect transmission rate	$1.0714 \times 10^{-2}\ \mathrm{d^{-1}}$
K	Half saturation rate of the pathogen	$10^6\,\mathrm{cells \cdot ml^{-1}}$
γ	Recovery rate	$(5\,\mathrm{d})^{-1}$
σ	Rate of host immunity loss	$(3 \times 365\,\mathrm{d})^{-1}$
K_P	Maximal carrying capacity of the pathogen	$2 \times 10^6\,\mathrm{cells \cdot ml^{-1}}$
δ	Bacterial death rate	$(30\,\mathrm{d})^{-1}$
ξ	Shedding rate	$50\,\mathrm{cells \cdot ml^{-1}p^{-1}d^{-1}}$
g	Intrinsic bacterial growth rate	$4.2857 \times 10^{-2}\,\mathrm{d^{-1}}$

Linearizing system (9)-(11) at the disease-free equilibrium $(N,0,0,0)$ with $N = \Lambda/d$, we obtain the following linear reaction-advection-diffusion system for I and P:

$$\begin{aligned}
&\frac{\partial I}{\partial t} = D_2\frac{\partial^2 I}{\partial x^2} + N\beta_1(x)I + N\frac{\beta_2(x)}{K}P - (d+\gamma)I,\\
&\frac{\partial P}{\partial t} = D_4\frac{\partial^2 P}{\partial x^2} - v\frac{\partial P}{\partial x} + \xi(x)I + g(x)P - \delta P,\\
&\frac{\partial I}{\partial x}(0,t) = \frac{\partial I}{\partial x}(1,t) = 0,\\
&\left(D_4\frac{\partial P}{\partial x} - vP\right)(0,t) = \left(D_4\frac{\partial P}{\partial x} - vP\right)(1,t) = 0,
\end{aligned}$$

for all $x \in [0,1]$ and $t > 0$. According to [39], we have

$$F(x) = \begin{pmatrix} N\beta_1(x) & N\beta_2(x)/K \\ \xi(x) & g(x) \end{pmatrix} \quad \text{and} \quad V = \begin{pmatrix} d+\gamma & 0 \\ 0 & \delta \end{pmatrix}$$

where F represents the new infection and V captures the transition.

Let $B = \operatorname{diag}\left(D_2\frac{\partial^2}{\partial x^2}, D_4\frac{\partial^2}{\partial x^2} - v\frac{\partial}{\partial x}\right) - V$. It follows from [39] that

$$R_0 = r(-\tilde{F}B^{-1}).$$

When the control effort is targeted at the human hosts, say through vaccination, the control set S would be $\{(1,1),(1,2)\}$. Then

$$F_S(x) = \begin{pmatrix} N\beta_1(x) & \frac{1}{K}N\beta_2(x) \\ 0 & 0 \end{pmatrix},\ V - (F(x) - F_S(x)) = \begin{pmatrix} d+\gamma & 0 \\ -\xi(x) & \delta - g(x) \end{pmatrix} \tag{12}$$

As discussed in [4], we make the following two assumptions:

(a) the pathogen can not survive in the environment in the absence of hosts (i.e., $g(x) < \delta$, $\forall x \in [0,1]$);
(b) the pathogen growth and shedding are assumed to be transitions within initial infectious state of human hosts.

Then the associated F and V would be replaced by F_S and $V - (F - F_S)$ defined in (12). According to Theorem 10 and Remark 4, the corresponding basic reproduction number is the same as the target reproduction number T_S, that is,

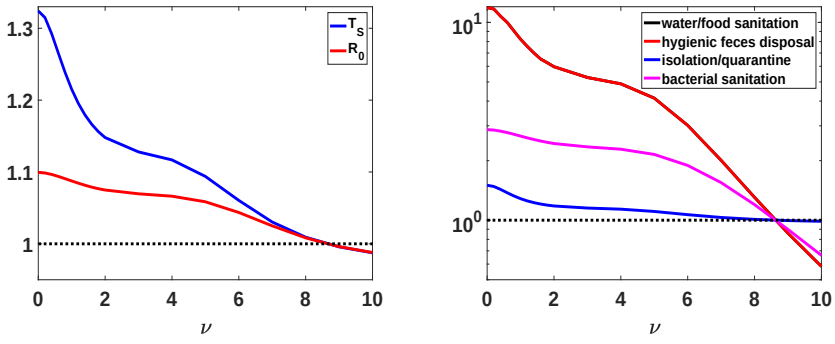
$$r\Big(-\tilde{F}_S\big(B + (\tilde{F} - \tilde{F}_S)\big)^{-1}\Big) = T_S. \tag{13}$$

As $S = \{(1,1),(1,2)\}$ is the entire first row, the target reproduction number T_S becomes the type reproduction number T_1. Biologically, T_1 can be interpreted as the expected number of secondary infections in host population produced by one infected human host in an otherwise susceptible population. In other words, the target reproduction number T_1 can be regarded as the basic reproduction number of a modified system, where the state of new infection is limited to the target control set and the infection from non-target set is considered as a part of the transition.

Figure 1 (a) displays the target reproduction number T_1 (blue curve) and the basic reproduction number R_0 (red curve) as the bacterial advection coefficient ν is varied, respectively. This result shows that (1) both T_1 and R_0 tend to decrease as the bacterial advection ν increases. Biologically, this indicates that if the bacterial advection rate ν is higher, then the bacterial transportation from the upstream to the downstream through the river flow become faster, which consequently reduces the human-to-pathogen contacts and leads to lower control effort and disease risk; (2) $T_1 - 1$ and $R_0 - 1$ have the same sign (see Theorem 9), which indicates that the target reproduction number T_1 and the basic reproduction number R_0 are equivalent threshold parameters provided that T_1 is well-defined. However, $T_1 > R_0$ when $R_0 > 1$, whereas $T_1 < R_0$ when $R_0 < 1$; (3) there is a critical value ν_* ($\nu_* \approx 8.6774$ in this case) such that $R_0 > 1$ (resp. $R_0 < 1$) when $0 \le \nu < \nu_*$ (resp. $\nu > \nu_*$). This implies that when infection risk is high (i.e., $R_0 > 1$), control is more demanding if the control effort is targeted at human vaccination alone instead

of the entire system. In contrast, less efforts are required to vaccination itself when infection risk is low (i.e., $R_0 < 1$).

Beside vaccination, cholera can also be successfully controlled by provision of clean water with adequate sanitation and appropriate hygienic disposal for human feces. If the hygienic feces disposal is employed, the target set $S = \{(2, 1)\}$. If adequate sanitation is applied with the aim in providing safe water and food, the associated target control set $S = \{(1, 2)\}$. Figure 1 (b) shows the values of these target reproduction numbers is a decreasing function of the bacterial advection rate ν. In view of Theorem 11, we have $T_{12} = T_{21}$. This is also verified numerically in Figure 1 (b), where the values T_{12} and T_{21} match quite well for the reaction-advection-diffusion model (9) (see the black and red curves) and the associated numerical difference is extremely small. Additionally, this disease may be controlled through isolation/quarantine of human hosts and bacterial sanitation (where the latter approach is used to reduce the growth rate of bacteria), for which the corresponding target control set is $S = \{(1, 1)\}$ and $S = \{(2, 2)\}$, respectively. Our result shows that $T_{12} = T_{21} > T_{22} > T_{11}$ when $R_0 > 1$ (or $0 \le \nu < \nu_*$), whereas $T_{12} = T_{21} < T_{22} < T_{11}$ when $R_0 < 1$ (or $\nu > \nu_0$). Interestingly, this indicates that isolation/quarantine requires the lowest effort among these four control strategies, as infection risk is high (i.e., $R_0 > 1$).



(a) vaccination (b) various control

Fig. 1 The target reproduction number T_S as a function of the advection coefficients ν. (a) Human vaccination $S = \{(1, 1), (1, 2)\}$. (b) Sanitation of drinking water and food preparation $S = \{(1, 2)\}$, hygienic feces disposal $S = \{(2, 1)\}$, isolation/quarantine $S = \{(1, 1)\}$ and bacterial sanitation $S = \{(2, 2)\}$, respectively. Note that the y-axis of (b) is plotted in log scale.

4.2 A spatial model for harmful algae

Blooms of harmful algae have become a great concern in water quality, particularly, of inland and coastal waters. Although strong flows in the main channel

of riverine reservoirs can wash out the harmful algae, shorelines and fringing coves constitute a hydraulic storage zone that may facilitate the persistence of algae. This motivates mathematical modeling and analysis of harmful algae dynamics, with the aim to further understand the longitudinal distribution of algal abundance and toxicity along the river flow and the algae persistence, see, e.g., [10,11,14,15,36].

A harmful algae model was proposed in [11] and analyzed in [15], which takes the form:

$$\begin{aligned}
\frac{\partial R}{\partial t} &= \delta\frac{\partial^2 R}{\partial x^2} - \nu\frac{\partial R}{\partial x} - q_N\big(f(R)-m\big)N + \alpha(R_S - R),\\
\frac{\partial N}{\partial t} &= \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + \big(f(R)-m\big)N,\\
\frac{\partial C}{\partial t} &= \delta\frac{\partial^2 C}{\partial x^2} - \nu\frac{\partial C}{\partial x} + \alpha(C_S - C) + \epsilon p(R,N) - kC,\\
\frac{\partial R_S}{\partial t} &= -\alpha\frac{A}{A_S}(R_S - R) - q_N\big(f(R_S)-m\big)N_S,\\
\frac{\partial N_S}{\partial t} &= -\alpha\frac{A}{A_S}(N_S - N) + \big(f(R_S)-m\big)N_S,\\
\frac{\partial C_S}{\partial t} &= -\alpha\frac{A}{A_S}(C_S - C) + \epsilon p(R_S,N_S) - kC_S,
\end{aligned} \tag{14}$$

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

$$\begin{aligned}
&\nu R(0,t) - \delta\frac{\partial R}{\partial x}(0,t) = \nu R^*,\\
&\nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \nu C(0,t) - \delta\frac{\partial C}{\partial x}(0,t) = 0,\\
&\frac{\partial U}{\partial x}(L,t) = 0, \quad U = R, N, C,
\end{aligned} \tag{15}$$

and initial conditions

$$U(x,0) = U^0(x) \geq 0, \quad 0 < x < L, \quad U = R,\, N,\, C,\, R_S,\, N_S,\, C_S. \tag{16}$$

Here $x\in[0,L]$ is the location variable along the longitudinal axis, $x=0$ represents the upstream end (e.g., headwaters), and $x=L$ is the downstream end (e.g., a dam or weir). The dissolved nutrient concentration, algal abundance and dissolved toxin concentration in the main flowing channel are denoted by $R(x,t)$, $N(x,t)$ and $C(x,t)$ with the unit μmol/L, μcells/mL, and μg/L, respectively. The corresponding quantities in the hydraulic storage zone are denoted with the subscript S. The first boundary condition in (15) specifies an inflowing nutrient with concentration R^*, the second boundary condition indicates no inflowing algae and toxin, and the last condition in (15) specifies a free-flow (Neumann) boundary condition at the downstream end for nutrient R, algae N and toxin C in the main channel. The usual example of the algal growth rate $f(R)$ follows a Monod function of the limiting nutrient concentration R, i.e., $f(R) = \frac{\mu_{max}R}{K+R}$, where μ_{max} is the maximal algal growth rate

Table 2 Definition of parameters of harmful algae model (14)

	Definition	Base value
δ	dispersion coefficient	$3 \times 10^5\,\mathrm{m}^2/\mathrm{day}$
ν	advection rate	varied
α	storage zone exchange rate	varied
$\frac{A}{A_S}$	cross-section ratio of main channel to storage zone	4
q_N	nutrient quota of algae	$1.39 \times 10^{-9}\mu$mol/cell
μ_{max}	maximal algal growth rate	$0.3\,/\mathrm{day}$
K	algal half saturation constant	$0.009\,\mu$mol/L
m	algal mortality rate	$0.1\,/\mathrm{day}$
ϵ	toxin production coefficient	$1.0 \times 10^{-8}\mu$g/cell
k	decay rate of toxin	$0.5\,/\mathrm{day}$
R^*	nutrient supply to reservoir	$1\,\mu$mol/L

are the maximal algal growth rate in the main channel and the storage zone, respectively and K is the half saturation constant. The production of toxins typically has two types [11]. As an illustrative example, we only consider the flagellate case (see [22] and the references therein) where the toxin production is assumed to be proportional to algae nutrient limitation and to algal abundance; namely, $\epsilon p(R,N) = \epsilon(\mu_{max} - f(R))N = \epsilon\dfrac{\mu_{max}K}{K+R}N$. The definition and base values of the parameters are provided in Table 2, where most of the base values of parameters are taken from [11]. Since the length of the reservoir (i.e., the main channel) L is likely highly variable. For simplicity, we set $L = 1,000$ m in our numerical simulation. For the purpose of algal control, we make a distinction between algal growth in two types of environments. Let $f_i(R) = \frac{\mu^i_{max}R}{K+R}$ for $i = 1, 2$. We use f_1 to capture the algal growth in the main reservoir and f_2 for that in the storage zone. Accordingly, μ^1_{max} and μ^2_{max} are the corresponding maximal growth rates. Moreover, $\mu^1_{max} = \mu^2_{max} = \mu_{max}$ are assumed.

Linearizing system (14)-(16) at the washout steady state (i.e., algae-toxin-free steady state) solution

$$(R, N, C, R_S, N_S, C_S) = (R^*, 0, 0, R^*, 0, 0)$$

yields a linear advection-dispersion-reaction system for the algae population:

$$\begin{aligned}
&\frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - \nu\frac{\partial N}{\partial x} + \alpha(N_S - N) + \big(f_1(R^*) - m\big)N, && 0 < x < L,\ t > 0,\\
&\frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + \big(f_2(R^*) - m\big)N_S, && 0 < x < L,\ t > 0,\\
&\nu N(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = \nu\frac{\partial N}{\partial x}(L,t) = 0, && t > 0,\\
&N(x,0) = N^0(x) \geq 0, \quad N_S(x,0) = N^0_S(x) \geq 0, && 0 < x < L.
\end{aligned}$$

In this case, the fertility matrix (also known as fecundity matrix) and transition matrix are given by

$$F(x) = \begin{pmatrix} f_1(R^*) & 0 \\ 0 & f_2(R^*) \end{pmatrix} \quad \text{and} \quad V = \begin{pmatrix} \alpha + m & -\alpha \\ -\alpha A/A_S & \alpha A/A_S + m \end{pmatrix}. \tag{17}$$

Let

$$B := \operatorname{diag}\left(\delta\frac{\partial^2}{\partial x^2} - \nu\frac{\partial}{\partial x}, 0\right) - V = \begin{pmatrix} \delta\dfrac{\partial^2}{\partial x^2} - \nu\dfrac{\partial}{\partial x} - (\alpha + m) & \alpha \\ \alpha A/A_S & -(\alpha A/A_S + m) \end{pmatrix}.$$

According to [15], the basic reproduction ratio for algae is

$$R_0 = r(-\tilde{F}B^{-1}).$$

By definition, the target reproduction number associated with the control set S is given by

$$T_S = r\Big(-\tilde{F}_S\big(B + (\tilde{F} - \tilde{F}_S)\big)^{-1}\Big). \tag{18}$$

In view of the diagonal form of $F(x)$, it follows from (18) that

$$\begin{aligned} T_{\{(1,1)\}} &= T_{\{(1,1),\,(2,1)\}} = T_{\{(1,1),\,(1,2)\}} =: T_1, \\ T_{\{(2,2)\}} &= T_{\{(1,2),\,(2,2)\}} = T_{\{(2,1),\,(2,2)\}} =: T_2. \end{aligned}$$

Thus, our investigation is focused on the target reproduction number for the algae in the storage zone (resp. the main reservoir); i.e., T_2 (resp. T_1). For instance, in the case of $T_2 = T_{\{(2,1),\,(2,2)\}}$, the corresponding control set $S = \{(2,1),(2,2)\}$, and

$$F_S(x) = \begin{pmatrix} 0 & 0 \\ 0 & f_2(R^*) \end{pmatrix} \quad \text{and} \quad V_S = \begin{pmatrix} \alpha + m - f_1(R^*) & -\alpha \\ -\alpha A/A_S & \alpha A/A_S + m \end{pmatrix}. \tag{19}$$

Moreover, T_2 can be regarded as the basic reproduction number of the corresponding linear system by replacing F and V defined in (17) with F_S and $V_S = V - (F - F_S)$, as defined in (19).

In Figure 2, T_1, T_2 and the basic reproduction ratio for algae,

$$R_0 = T_{\{(1,1),(1,2),(2,1),(2,2)\}},$$

are compared. First of all, it shows that these three target reproduction numbers stay on the same side of the unity. By [15, Theorem 3.2], system (14)-(16) admits a threshold dynamics. More precisely, if $R_0 \leq 1$, the washout steady state is globally asymptotically stable; if $R_0 > 1$, the unique coexistence steady state is globally asymptotically stable and the algae persists. Therefore, our result numerically verifies Theorem 9 and indicates that these three target reproduction numbers are equivalent as a sharp threshold quantity in terms of the persistence of algae, provided that they are well-defined. Secondly, Figure 2 illustrates the influence of the advection coefficient ν and the exchange rate between main channel and storage zone α on these target reproduction

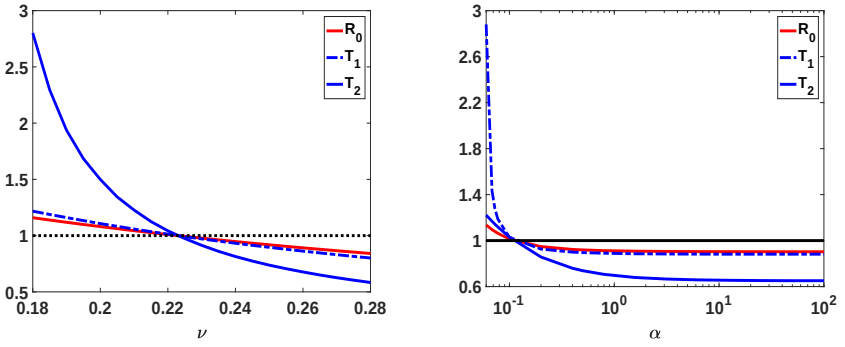


Fig. 2 Compare T_1, T_2 and the basic reproduction number R_0 as parameter p is varied. (a) $p = \nu$ (i.e., advection coefficient) with $\alpha = 0.5$ day^{-1}. (b) $p = \alpha$ (i.e., storage zone exchange rate as compared to the main channel) with $\nu = 0.25$ km/day. Note that the horizontal axis of Figure (b) is plotted in the log scale.

numbers. Particularly, Figure 2 (a) plots T_1, T_2 and R_0 as a function of the advection coefficient ν, when the storage zone exchange rate $\alpha = 0.5$ day^{-1}. In this case, as ν is larger, the values of T_1, T_2 and R_0 shrink, and they cross the unity at a critical value $\nu^* \approx 0.2225$ km/day. Note that the advection is caused by the system dilution for a given reservoir. This result implies that the stronger dilution process tends to decrease the fertility control effort needed for algae. Besides, the severity of the required control effort appears to be the highest in the storage zone, followed by the main reservoir and the lowest in the entire system (i.e., $T_2 > T_1 > R_0 > 1$) when $\nu < \nu^*$; whereas the situation is reversed when $\nu > \nu^*$. Meanwhile, Figure 2 (b) shows that T_1, T_2 and R_0 are decreasing functions of the storage zone exchange rate α, when $\nu = 0.25$ km/day. There exists a critical value α^* (in this case $\alpha^* \approx 0.10$ day^{-1}). As α goes above α^*, it drives all these three target reproduction numbers below one. Moreover, $T_1 > T_2$ when $\alpha < \alpha^*$; $T_1 < T_2$ when $\alpha > \alpha^*$. This indicates that when the algal control effort in the main channel is compared to that in the storage zone, the main channel requires more efforts if the storage zone exchange rate α is sufficiently small (i.e., $\alpha < \alpha^*$); otherwise (i.e., $\alpha > \alpha^*$), the storage zone is more demanding from the viewpoint of the fertility control.

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