

## **Basic Reproduction Ratios for Periodic Compartmental Models with Time Delay**

**Xiao-Qiang Zhao**

Received: 19 October 2014 / Revised: 2 January 2015 / Published online: 21 January 2015 © Springer Science+Business Media New York 2015

**Abstract** In this paper, we establish the theory of basic reproduction ratio  $R_0$  for a large class of time-delayed compartmental population models in a periodic environment. It is proved that  $R_0$  serves as a threshold value for the stability of the zero solution of the associated periodic linear systems. As an illustrative example, we also apply the developed theory to a periodic SEIR model with an incubation period and obtain a threshold result on its global dynamics in terms of  $R_0$ .

**Keywords** Compartmental models · Time delay · Periodicity · Reproduction ratio · Threshold dynamics

**Mathematics Subject Classification** 34K20 · 37B55 · 92D30

### **1 Introduction**

The basic reproduction number (ratio)  $R_0$  is one of the most important concepts in population biology. In epidemiology, *R*<sup>0</sup> is the expected number of secondary cases produced, in a completely susceptible population, by a typical infective individual, and  $R_0$  is also a commonly used measure of the effort needed to control an infectious disease. Diekmann et al. [\[9](#page-15-0)] introduced the next generation operators approach to  $R_0$  for autonomous models, and Van den Driessche and Watmough [\[23\]](#page-15-1) developed the theory of *R*<sup>0</sup> for ordinary differential equations (ODE) models with compartmental structure. These two works have found numerous applications in the study of various infectious disease models. For population models in a periodic environment, Bacaër and Guernaoui [\[3](#page-14-0)] proposed a general definition of *R*0, that is,  $R_0$  is the spectral radius of an integral operator on the space of continuous periodic functions. Wang and Zhao  $[24]$  characterized  $R_0$  for periodic compartmental ODE models and proved

 $X.-Q.$  Zhao  $(\boxtimes)$ 

Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada e-mail: zhao@mun.ca

that it is a threshold parameter for the local stability of the disease-free periodic solution. Further, Thieme [\[22\]](#page-15-3) presented the theory of spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity. Bacaër and Ait Dads [\[1](#page-14-1)[,2\]](#page-14-2) also found a more biological interpretation of  $R_0$  for periodic models and showed that it is the asymptotic ratio of total infections in two successive generations of the infection tree. More recently, Inaba [\[12\]](#page-15-4) introduced the concept of a generation evolution operator to give a new definition of  $R_0$  for structured populations in heterogeneous environments, which unifies two definitions in [\[3](#page-14-0)[,9\]](#page-15-0) and has intuitively clear biological meaning.

Once  $R_0$  is introduced for an epidemic model, it is usually expected that the disease cannot invade the disease-free state if  $R_0 < 1$  and can invade if  $R_0 > 1$ . Mathematically, this means that the sign of  $R_0 - 1$  determines the stability of the zero solution of a linear system associated with infectious variables. In this regard, the theory developed in [\[22\]](#page-15-3) provides a powerful tool, see, e.g., [\[10,](#page-15-5)[16](#page-15-6)[,17,](#page-15-7)[25](#page-15-8)[,26\]](#page-15-9)) for autonomous reaction-diffusion models with or without time delay, and [\[27\]](#page-15-10) for almost periodic compartmental ODE models. However, it is much more difficult to apply abstract results of [\[22](#page-15-3)] to periodic and time-delayed population models with or without spatial diffusion. For some specific periodic models, one may derive linear periodic Volterra integral equations for infectious variables and then utilize the renewal theory (see, e.g., [\[1](#page-14-1),[21\]](#page-15-11) and references therein) after a careful verification of certain technical conditions (see, e.g., [\[18](#page-15-12)] and references therein). The purpose of this paper is to establish the theory of basic reproduction ratio  $R_0$  for periodic and time-delayed population models with compartmental structure. Motivated by an eigenvalue problem associated with the renewal theory, we introduce a one-parameter family of positive linear operators on the space of continuous periodic functions and study the properties of their spectral radii as the parameter varies. These preparatory results are then employed to prove the aforementioned stability result in terms of  $R_0$ . It is worthy to point out that our approach also applies to abstract delay differential equations (and hence, periodic and time-delayed reaction-diffusion models), see Remark [2.1](#page-10-0) below.

The rest of this paper is organized as follows. In the next section, we first introduce the basic reproduction ratio  $R_0$  for periodic compartmental models with time delay, then prove the stability result (Theorem [2.1\)](#page-8-0) and give a characterization of *R*<sup>0</sup> (Theorem [2.2\)](#page-8-1). We also obtain an explicit formula for *R*<sup>0</sup> in the autonomous case (Corollary [2.1\)](#page-9-0). In Sect. [3,](#page-10-1) we apply the theory of  $R_0$  in Sect. [2,](#page-1-0) together with the persistence theory for periodic semiflows (see, e.g., [\[30\]](#page-15-13)), to a periodic SEIR model of a disease transmission, and establish a threshold type result on its global dynamics in terms of  $R_0$ . It is hoped that the theory of  $R_0$  developed in this paper will find more applications in time-delayed compartmental population models such as those with distributed delays, spatial dispersal, or time-dependent delays.

#### <span id="page-1-0"></span>**2 Basic Reproduction Ratio**

Let  $\tau \ge 0$  be a given number,  $C = C([- \tau, 0], \mathbb{R}^m)$ , and  $C^+ = C([- \tau, 0], \mathbb{R}^m_+)$ . Then  $(C, C<sup>+</sup>)$  is an ordered Banach space equipped with the maximum norm and the positive cone  $C^+$ . Let  $F : \mathbb{R} \to \mathcal{L}(C, \mathbb{R}^m)$  be a map and  $V(t)$  be a continuous  $m \times m$  matrix function on R. Assume that  $F(t)$  and  $V(t)$  are  $\omega$ -periodic in *t* for some real number  $\omega > 0$ . For a continuous function  $u : [-\tau, \sigma) \to \mathbb{R}^m$  with  $\sigma > 0$ , define  $u_t \in C$  by

$$
u_t(\theta) = u(t + \theta), \quad \forall \theta \in [-\tau, 0]
$$

for any  $t \in [0, \sigma)$ .

<span id="page-2-0"></span>We consider a linear and periodic functional differential system:

$$
\frac{du(t)}{dt} = F(t)u_t - V(t)u(t), \quad t \ge 0.
$$
\n(2.1)

System [\(2.1\)](#page-2-0) may come from the equations of infectious variables in the linearization of a given ω-periodic and time-delayed compartmental epidemic model at a disease-free ωperiodic solution. As such, *m* is the total number of the infectious compartments, and the newly infected individuals at time *t* depend linearly on the infectious individuals over the time interval  $[t - \tau, t]$ , which is described by  $F(t)u_t$ . Further, the internal evolution of individuals in the infectious compartments (e.g., natural and disease-induced deaths, and movements among compartments) is governed by the linear ordinary differential system:

$$
\frac{du(t)}{dt} = -V(t)u(t).
$$
\n(2.2)

<span id="page-2-1"></span>Of course, we may also obtain system  $(2.1)$  by linearizing a population growth model with *m* patches (or types) at its zero solution, where the word "birth" should be used to replace "infection".

Throughout this section, we assume that  $F(t): C \to \mathbb{R}^m$  is given by

$$
F(t)\phi = \int_{-\tau}^{0} d[\eta(t,\theta)]\phi(\theta), \quad \forall t \in \mathbb{R}, \phi \in C,
$$

where  $\eta(t,\theta)$  is an  $m \times m$  matrix function which is measurable in  $(t,\theta) \in \mathbb{R} \times \mathbb{R}$  and normalized so that  $\eta(t,\theta) = 0$  for all  $\theta \ge 0$  and  $\eta(t,\theta) = \eta(t,-\tau)$  for all  $\theta \le -\tau$ . Further,  $\eta(t,\theta)$  is continuous from the left in  $\theta$  on ( $-\tau$ , 0) for each *t*, and the variation of  $\eta(t,\cdot)$ on  $[-\tau, 0]$  satisfies  $Var_{[-\tau,0]} \eta(t, \cdot) \leq m(t)$  for some  $m \in \mathcal{L}_1^{\text{loc}}((-\infty,\infty), \mathbb{R})$ , the space of functions from  $(-\infty, \infty)$  into R that are Lebesgue integrable on each compact set of (−∞,∞). Since *F*(*t*) is ω-periodic in *t*, we have

$$
\sup_{t\in\mathbb{R}}\|F(t)\|=\sup_{0\leq t\leq\omega}\|F(t)\|\leq \sup_{0\leq t\leq\omega}m(t).
$$

By the general theory of linear functional differential equations in [\[11,](#page-15-14) Section 8.1], it follows that for any  $s \in \mathbb{R}$  and  $\phi \in C$ , system [\(2.1\)](#page-2-0) has a unique solution  $u(t, s, \phi)$  on [ $s, \infty$ ) with  $u_s = \phi$ . We define the evolution operators  $U(t, s)$  on *C* associated with [\(2.1\)](#page-2-0) as

$$
U(t,s)\phi=u_t(s,\phi),\ \forall \phi\in C,\ t\geq s,\ s\in\mathbb{R},
$$

where  $u_t(s, \phi)(\theta) = u(t + \theta, s, \phi)$ ,  $\forall \theta \in [-\tau, 0]$ . Then each operator  $U(t, s)$  is continuous and

$$
U(s, s) = I, \ U(t, s)U(s, r) = U(t, r), \ U(t + \omega, s + \omega) = U(t, s), \ \forall t \ge s \ge r. \tag{2.3}
$$

Let  $\Phi(t, s)$ ,  $t \geq s$ , be the evolution matrices associated with system [\(2.2\)](#page-2-1), that is,  $\Phi(t, s)$ satisfies

$$
\frac{\partial}{\partial t}\Phi(t,s)=-V(t)\Phi(t,s), \ \forall t\geq s, \text{ and } \Phi(s,s)=I, \ \forall s\in\mathbb{R},
$$

and  $\omega(\Phi)$  be the exponential growth bound of  $\Phi(t, s)$ , that is,

$$
\omega(\Phi) = \inf \left\{ \tilde{\omega} : \exists M \ge 1 \text{ such that } \|\Phi(t+s,s)\| \le Me^{\tilde{\omega}t}, \forall s \in \mathbb{R}, t \ge 0 \right\}.
$$

In order to introduce the basic reproduction ratio for system [\(2.1\)](#page-2-0), throughout this section we always assume that

- (H1) Each operator  $F(t): C \to \mathbb{R}^m$  is positive in the sense that  $F(t)C^+ \subseteq \mathbb{R}^m_+$ .
- (H2) Each matrix  $-V(t)$  is cooperative, and  $\omega(\Phi) < 0$ .

In view of the periodic environment, we supposed that  $v(t)$ ,  $\omega$ -periodic in *t*, is the initial distribution of infectious individuals. For any given  $s \geq 0$ ,  $F(t - s)v_{t-s}$  is the distribution of newly infected individuals at time  $t - s$ , which is produced by the infectious individuals who were introduced over the time interval  $[t - s - \tau, t - s]$ . Then  $\Phi(t, t - s) F(t - s) v_{t-s}$ is the distribution of those infected individuals who were newly infected at time *t* − *s* and remain in the infected compartments at time *t*. It follows that

$$
\int_0^\infty \Phi(t, t-s) F(t-s) v_{t-s} ds = \int_0^\infty \Phi(t, t-s) F(t-s) v(t-s+\cdot) ds
$$

is the distribution of accumulative new infections at time *t* produced by all those infectious individuals introduced at all previous times to *t*.

Note that for any given  $s \geq 0$ ,  $\Phi(t, t - s)v(t - s)$  gives the distribution of those infectious individuals who were introduced at time  $t - s$  and remain in the infected compartments at time *t*, and hence,  $w(t) := \int_0^\infty \Phi(t, t - s)v(t - s)ds$  is the distribution of accumulative infectious individuals who were introduced at all previous times to *t* and remain in the infected compartments at time *t*. Thus, the distribution of newly infected individuals at time *t* is

$$
F(t)w_t = F(t)\left(\int_0^\infty \Phi(t+\cdot,t-s+\cdot)v(t-s+\cdot)ds\right).
$$

Let  $C_{\omega}$  be the ordered Banach space of all continuous and  $\omega$ -periodic functions from R to  $\mathbb{R}^m$ , which is equipped with the maximum norm and the positive cone  $C^+_{\omega} := \{v \in C_{\omega} :$  $v(t) \geq 0$ ,  $\forall t \in \mathbb{R}$ . Then we can define two linear operators on  $C_{\omega}$  by

$$
[Lv](t) = \int_0^\infty \Phi(t, t-s)F(t-s)v(t-s+\cdot)ds, \ \forall t \in \mathbb{R}, \ v \in C_\omega,
$$

and

$$
[\hat{L}v](t) = F(t) \left( \int_0^\infty \Phi(t + \cdot, t - s + \cdot)v(t - s + \cdot) ds \right), \ \forall t \in \mathbb{R}, \ v \in C_\omega.
$$

Let *A* and *B* be two bounded linear operators on  $C_{\omega}$  defined by

$$
[Av](t) = \int_0^\infty \Phi(t, t-s)v(t-s)ds, [Bv](t) = F(t)v_t, \forall t \in \mathbb{R}, v \in C_\omega.
$$

It then follows that  $L = A \circ B$  and  $\hat{L} = B \circ A$ , and hence, *L* and  $\hat{L}$  have the same spectral radius.

Motivated by the concept of next generation operators in  $[3,9,22-24]$  $[3,9,22-24]$  $[3,9,22-24]$  $[3,9,22-24]$ , we define the spectral radius of  $L$  and  $\hat{L}$  as the basic reproduction ratio

$$
R_0 := r(L) = r(\tilde{L}).
$$

for periodic system [\(2.1\)](#page-2-0).

For any given  $\lambda \in \mathbb{R}$ , let  $E_{\lambda}$  be a linear operator on *C* defined by

$$
[E_{\lambda}\phi](\theta) = e^{\lambda\theta}\phi(\theta), \ \forall \theta \in [-\tau, 0], \ \phi \in C.
$$

<span id="page-3-0"></span>It then easily follows that  $||E_\lambda|| \leq \max\{1, e^{-\lambda \tau}\}, \forall \lambda \in \mathbb{R}$ . Now we introduce a family of linear operators  $L_{\lambda}$  on  $C_{\omega}$ :

$$
[L_{\lambda}v](t) = \int_0^{\infty} e^{-\lambda s} \Phi(t, t - s) F(t - s) E_{\lambda} v(t - s + \cdot) ds, \ \forall t \in \mathbb{R}, \ v \in C_{\omega}.
$$
 (2.4)

<span id="page-4-2"></span>Clearly,  $L_0 = L$ , and  $L_\lambda$  is well defined for all  $\lambda > \omega(\Phi)$ . Further, we have the following observation.

**Lemma 2.1** *For each*  $\lambda > \omega(\Phi)$ *, the operator*  $L_{\lambda}$  *is positive, continuous and compact on C*ω*.*

*Proof* Let  $\lambda > \omega(\Phi)$  be given. Clearly,  $E_{\lambda}$  is a positive linear operator on *C*. By virtue of (H1) and (H2),  $F(t)$  and  $\Phi(t, s)$  ( $t \geq s$ ) are positive linear operators. This implies that  $L_{\lambda}$  is positive on  $C_{\omega}$ . Since  $\omega(\Phi) < 0$  and

 $\|\Phi(t, t-s)F(t-s)E_\lambda\| \leq M_0e^{\omega(\Phi)s} \cdot \sup_{0 \leq t \leq t} m(r) \cdot \|E_\lambda\|, \ \forall t \in \mathbb{R}, \ s \in [0, \infty),$ 0≤*r*≤ω

for some  $M_0 > 0$ , we see that  $L_\lambda$  is bounded, and hence, continuous on  $C_\omega$ . In view of

$$
[L_{\lambda}v](t)=\int_{-\infty}^{t}e^{-\lambda(t-s)}\Phi(t,s)F(s)E_{\lambda}v_{s}ds, \quad \forall t \in \mathbb{R}, \ v \in C_{\omega},
$$

<span id="page-4-0"></span>we easily obtain

$$
\frac{d}{dt}[L_{\lambda}v](t) = F(t)E_{\lambda}v_t - (V(t) + \lambda I)[L_{\lambda}v](t), \quad \forall t \in \mathbb{R}, \ v \in C_{\omega}.
$$
 (2.5)

It then follows that for any  $a > 0$ , there exists  $K = K(a) > 0$  such that  $|\frac{d}{dt}[L_\lambda v](t)| \leq K$ for all  $t \in [0, \omega]$  and  $v \in C_{\omega}$  with  $||v|| \le a$ . Thus, the Ascoli-Arzela theorem implies that  $L_1$  is compact on  $C_{\omega}$ .  $L_{\lambda}$  is compact on  $C_{\omega}$ .

Let  $M_0 > 0$  be fixed such that  $\|\Phi(t, s)\| \leq M_0 e^{\omega(\Phi)(t-s)}$ ,  $\forall t \geq s$ . For any given  $\epsilon > 0$ , we set  $V_{\epsilon}(t) = V(t) - \epsilon E$ , where *E* is the *m* × *m* matrix with each element being 1. Let  $\Phi_{\epsilon}(t, s)$ be the evolution operators associated with the linear periodic system  $\frac{du(t)}{dt} = -V_{\epsilon}(t)u(t)$ . Then we have the following estimate.

<span id="page-4-1"></span>**Lemma 2.2** *Let*  $c = \epsilon M_0 ||E||$ *. Then for any*  $\epsilon > 0$ *, there holds* 

$$
\|\Phi_{\epsilon}(t,t-s)-\Phi(t,t-s)\|\leq cM_0se^{(\omega(\Phi)+c)s},\ \forall t\in\mathbb{R},\ s\geq 0.
$$

*Proof* By the constant-variation formula, we obtain

$$
\Phi_{\epsilon}(t,s)x=\Phi(t,s)x+\int_{s}^{t}\Phi(t,r)\epsilon E\Phi_{\epsilon}(r,s)xdr, \ \forall t\geq s, \ s\in\mathbb{R}, \ x\in\mathbb{R}^{m}.
$$

This implies that  $\Phi_{\epsilon}(t,s)$  satisfies the abstract Volterra integral equation:

$$
\Phi_{\epsilon}(t,s) = \Phi(t,s) + \int_{s}^{t} \Phi(t,r) \epsilon E \Phi_{\epsilon}(r,s) dr, \ \forall t \geq s, \ s \in \mathbb{R}.
$$
 (2.6)

Let  $h_1(t, s) := \Phi(t, s) \in E$ , and define

$$
h_n(t,s) = \int_s^t h_1(t,r)h_{n-1}(r,s)dr, \ \forall n \ge 2.
$$

Since  $||h_1(t, s)|| \leq ce^{\omega(\Phi)(t-s)}$ ,  $\forall t \geq s, s \in \mathbb{R}$ , it follows from an induction argument that

$$
||h_n(t,s)|| \leq \frac{c^n}{(n-1)!} e^{\omega(\Phi)(t-s)} (t-s)^{n-1}, \forall n \geq 1, t \geq s, s \in \mathbb{R},
$$

 $\circled{2}$  Springer

and hence,  $\sum_{n=1}^{\infty} ||h_n(t,s)|| \le ce^{(\omega(\Phi)+c)(t-s)}$ . Thus, the linear operator  $h(t,s) :=$ <br> $\sum_{n=1}^{\infty} h_n(t,s)$  is well defined for any  $t > s$ ,  $s \in \mathbb{R}$ , and  $||h(t,s)|| < ce^{(\omega(\Phi)+c)(t-s)}$ . By

 $\sum_{n=1}^{\infty} h_n(t, s)$  is well defined for any  $t \geq s, s \in \mathbb{R}$ , and  $||h(t, s)|| \leq ce^{(\omega(\Phi)+c)(t-s)}$ . By the proof of [\[7](#page-14-3), Theorem 9.1],  $\Phi_{\epsilon}(t, s)$  can be represented as

$$
\Phi_{\epsilon}(t,s) = \Phi(t,s) + \int_{s}^{t} h(t,r)\Phi(r,s)dr, \ \forall t \geq s, \ s \in \mathbb{R}.
$$
 (2.7)

It then follows that

$$
\begin{aligned} \|\Phi_{\epsilon}(t,t-s) - \Phi(t,t-s)\| &\leq \int_{t-s}^{t} \|h(t,r)\| \cdot \|\Phi(r,t-s)\| dr \\ &\leq \int_{t-s}^{t} c e^{(\omega(\Phi)+c)(t-r)} M_0 e^{\omega(\Phi)(r-(t-s))} dr \\ &= M_0 e^{\omega(\Phi)s} (e^{cs}-1) \\ &\leq c M_0 s e^{(\omega(\Phi)+c)s}, \ \forall t \in \mathbb{R}, \ s \geq 0. \end{aligned}
$$

Here we have used the inequality that  $e^{cs} - 1 \leq c s e^{cs}$ ,  $\forall s \geq 0$ .

<span id="page-5-0"></span>For any  $\lambda > \omega(\Phi)$ , let  $\mu(\lambda)$  be the spectral radius of  $L_{\lambda}$ , that is,  $\mu(\lambda) := r(L_{\lambda})$ . Then we have the following two results on properties of the function  $\mu(\lambda)$ .

#### **Proposition 2.1** *The following statements are valid:*

*(i)*  $\mu(\lambda)$  *is continuous and nonincreasing on*  $(\omega(\Phi), \infty)$ *, and*  $\mu(\infty) = 0$ *. (ii)*  $\mu(\lambda) = 1$  *has at most one solution in*  $(\omega(\Phi), \infty)$ *.* 

*Proof* (i) Let  $\lambda_0 \in (\omega(\Phi), \infty)$  be given and choose a small number  $\delta > 0$  such that  $[\lambda_0 \delta$ , λ<sub>0</sub> + δ] ⊂ (ω(Φ), ∞). It is easy to see that

$$
||E_{\lambda}-E_{\lambda_0}||\leq \tau \max\{1,e^{-(\lambda_0-\delta)\tau}\}|\lambda-\lambda_0|, \ \forall \lambda\in [\lambda_0-\delta,\lambda_0+\delta].
$$

As a result, there exist two positive numbers  $K_1$  and  $K_2$  such that for any  $\lambda \in [\lambda_0 - \delta, \lambda_0 + \delta]$ , we have

$$
||L_{\lambda} - L_{\lambda_0}|| \leq K_1 \int_0^{\infty} |e^{-\lambda s} - e^{-\lambda_0 s}| e^{\omega(\Phi)s} ds
$$
  
+K\_2|\lambda - \lambda\_0| \int\_0^{\infty} e^{-\lambda\_0 s} e^{\omega(\Phi)s} ds  

$$
\leq K_1 |\lambda - \lambda_0| \int_0^{\infty} s e^{-(\lambda_0 - \delta)s} e^{\omega(\Phi)s} ds
$$
  
+K\_2|\lambda - \lambda\_0| \int\_0^{\infty} e^{-\lambda\_0 s} e^{\omega(\Phi)s} ds  

$$
= \frac{K_1 |\lambda - \lambda_0|}{(\lambda_0 - \delta - \omega(\Phi))^2} + \frac{K_2 |\lambda - \lambda_0|}{\lambda_0 - \omega(\Phi)}.
$$

This implies that  $\lim_{\lambda\to\lambda_0} ||L_\lambda - L_{\lambda_0}|| = 0$ . By the continuity of spectral radius for compact linear operators (see, e.g., [\[8](#page-14-4), Theorem 2.1(a)]), we then obtain that  $\lim_{\lambda \to \lambda_0} \mu(\lambda) = \mu(\lambda_0)$ . Thus,  $\mu(\lambda)$  is continuous on  $(\omega(\Phi), \infty)$ . It is easy to verify that

$$
[L_{\lambda_1}v](t) \ge [L_{\lambda_2}v](t), \ \forall \omega(\Phi) < \lambda_1 \le \lambda_2, \ t \in \mathbb{R}, \ v \in C_{\omega}^+.
$$

Since each  $L_{\lambda}$  is a positive and bounded linear operator on  $C_{\omega}$ , [\[4](#page-14-5), Theorem 1.1] implies that  $\mu(\lambda) = r(L_\lambda)$  is a nonincreasing function of  $\lambda$  on  $(\omega(\Phi), \infty)$ . Note that  $\|\Phi(t, s)\| \leq$ 

 $M_0e^{\omega(\Phi)(t-s)}$ ,  $\forall t \geq s$ , and  $||E_\lambda|| \leq 1$ ,  $\forall \lambda \geq 0$ . It then follows that

$$
||L_\lambda|| \leq M_0 \sup_{0 \leq t \leq \omega} ||F(t)|| \int_0^\infty e^{-\lambda s} e^{\omega(\Phi)s} ds = \frac{M_0 \sup_{0 \leq t \leq \omega} ||F(t)||}{\lambda - \omega(\Phi)}, \ \forall \lambda \geq 0.
$$

In view of  $0 \le \mu(\lambda) = r(L_{\lambda}) \le ||L_{\lambda}||$ , we obtain  $\mu(\infty) = \lim_{\lambda \to \infty} \mu(\lambda) = 0$ .

(ii) Assume, by contradiction, that  $\mu(\lambda) = 1$  has two solutions  $\lambda_1 < \lambda_2$  in  $(\omega(\Phi), \infty)$ . Since  $\mu(\lambda)$  is nonincreasing on  $(\omega(\Phi), \infty)$ , we must have  $\mu(\lambda) = 1$ ,  $\forall \lambda \in [\lambda_1, \lambda_2]$ . Let  $\lambda \in [\lambda_1, \lambda_2]$  be given. Since  $L_\lambda$  is a positive and compact linear operator on  $C_\omega$  and  $r(L_\lambda)$  =  $\mu(\lambda) = 1 > 0$ , the Krein–Rutman theorem implies that  $L_{\lambda}v = v$  for some  $v \in C_{\omega}^{+} \setminus \{0\}$ . By virtue of  $(2.5)$ , we obtain

$$
\frac{d}{dt}v(t) = F(t)E_{\lambda}v_t - (V(t) + \lambda I)v(t), \quad \forall t \in \mathbb{R}.
$$

Let  $u(t) := e^{\lambda t} v(t)$ . Since  $u_t = e^{\lambda t} E_\lambda v_t$ ,  $\forall t \in \mathbb{R}$ , it follows from a straightforward computation that

$$
\frac{d}{dt}u(t) = F(t)u_t - V(t)u(t), \quad \forall t \in \mathbb{R}.
$$

Set  $\phi := u_0 = E_\lambda v_0$ . Then  $U(t, 0)\phi = u_t$ ,  $\forall t \geq 0$ , which implies that  $\phi \in C^+ \setminus \{0\}$ since  $u(\cdot) \neq 0$  on  $[0, \infty)$ . Clearly, the  $\omega$ -periodicity of  $v(t)$  yields  $v_{t+\omega} = v_t$ ,  $\forall t \in \mathbb{R}$ . In particular, we have

$$
U(\omega, 0)\phi = u_{\omega} = e^{\lambda \omega} E_{\lambda} v_{\omega} = e^{\lambda \omega} E_{\lambda} v_0 = e^{\lambda \omega} \phi.
$$

It follows that  $e^{\lambda \omega}$  is an eigenvalue of  $U(\omega, 0)$ , and hence,  $e^{\lambda n \omega}$  is an eigenvalue of  $U(n\omega, 0) = (U(\omega, 0))^n$  for any integer  $n \ge 1$ . Now we fix an integer  $n_0 > 0$  such that  $n_0 \omega > \tau$ . By [\[11](#page-15-14), Theorem 3.6.1], the operator  $U(n_0 \omega, 0)$  is compact on *C*. Thus,  $e^{\lambda n_0 \omega}$  is an eigenvalue of  $U(n_0\omega, 0)$  for all  $\lambda \in [\lambda_1, \lambda_2]$ . But this is impossible since the compact linear operator  $U(n_0\omega, 0)$  has only countablely many eigenvalues. linear operator  $U(n_0\omega, 0)$  has only countablely many eigenvalues.

# <span id="page-6-2"></span>**Proposition 2.2** *If*  $r(U(\omega, 0)) > r(\Phi(\omega, 0))$ *, then*  $\lambda^* := \frac{\ln r(U(\omega, 0))}{\omega}$  *satisfies*  $\mu(\lambda^*) = 1$ *.*

*Proof* For any given  $\epsilon > 0$ , let  $V_{\epsilon}(t)$  and  $\Phi_{\epsilon}(t, s)$  be defined as in Lemma [2.2,](#page-4-1) and define  $F_{\epsilon}(t)\phi = F(t)\phi + \epsilon\phi(-\tau)$ ,  $\forall \phi \in C$ . We consider small perturbations of system [\(2.1\)](#page-2-0):

$$
\frac{du(t)}{dt} = F_{\epsilon}(t)u_t - V_{\epsilon}(t)u(t), \quad t \ge 0.
$$
\n(2.8)

<span id="page-6-0"></span>Let  $U_{\epsilon}(t, s)$  be the evolution operators associated with the linear functional differential system [\(2.8\)](#page-6-0). By [\[22,](#page-15-3) Proposition A.2], it follows that  $\omega(\Phi_{\epsilon}) = \frac{\ln r(\Phi_{\epsilon}(\omega,0))}{\omega}$ . Since  $\omega(\Phi) < 0$ , we have  $\omega(\Phi_{\epsilon})$  < 0 for sufficiently small  $\epsilon > 0$ . Let  $L^{\epsilon}_{\lambda}$  be defined as in [\(2.4\)](#page-3-0) with  $F(t)$ and  $\Phi(t, s)$  replaced by  $F_{\epsilon}(t)$  and  $\Phi_{\epsilon}(t, s)$ , respectively. By [\[19,](#page-15-15) Lemma 5.3.2],  $U_{\epsilon}(t, 0)$ is strongly positive on *C* for any  $t \geq (m + 1)\tau$ . Choose an integer  $n_0 > 0$  such that  $n_0\omega \geq (m+1)\tau$ . Since  $(U_\epsilon(\omega, 0))^{n_0} = U_\epsilon(n_0\omega, 0)$  is compact and strongly positive, [\[14,](#page-15-16) Lemma 3.1] implies that  $r(U_\epsilon(\omega, 0))$  is a simple eigenvalue of  $U_\epsilon(\omega, 0)$  having a strongly positive eigenvector, and the modulus of any other eigenvalue is less than  $r(U_{\epsilon}(\omega, 0))$ . Let  $\hat{\lambda}_{\epsilon}^* := \frac{\ln r(U_{\epsilon}(\omega,0))}{\omega}$ . By the proof of [\[29,](#page-15-17) Proposition 2.1], it then follows that there is positive *ω*-periodic function  $v^{\epsilon}(t)$  such that  $u^{\epsilon}(t) = e^{\lambda_{\epsilon}^{*} t} v^{\epsilon}(t)$  is a positive solution of [\(2.8\)](#page-6-0) for all  $t \in \mathbb{R}$ . Thus, the constant-variation formula yields

<span id="page-6-1"></span>
$$
u^{\epsilon}(t) = \Phi_{\epsilon}(t, r)u^{\epsilon}(r) + \int_{r}^{t} \Phi_{\epsilon}(t, s)F_{\epsilon}(s)u^{\epsilon}_{s}ds, \ \forall t \ge r, \ r \in \mathbb{R}.
$$
 (2.9)

<span id="page-7-0"></span>On substituting  $u^{\epsilon}(t) = e^{\lambda_{\epsilon}^{*}t} v^{\epsilon}(t)$  into [\(2.9\)](#page-6-1), we obtain

$$
v^{\epsilon}(t) = e^{-\lambda_{\epsilon}^{*}(t-r)} \Phi_{\epsilon}(t,r) v^{\epsilon}(r) + \int_{r}^{t} e^{-\lambda_{\epsilon}^{*}(t-s)} \Phi_{\epsilon}(t,s) F_{\epsilon}(s) E_{\lambda_{\epsilon}^{*}} v_{s}^{\epsilon} ds \qquad (2.10)
$$

for all  $t > r$ ,  $r \in \mathbb{R}$ . Since  $\lim_{\epsilon \to 0^+} (r(U_{\epsilon}(\omega, 0)) - r(\Phi_{\epsilon}(\omega, 0))) = r(U(\omega, 0))$  $r(\Phi(\omega, 0)) > 0$ , it follows that  $r(U_{\epsilon}(\omega, 0)) - r(\Phi_{\epsilon}(\omega, 0)) > 0$ , and hence,  $\lambda_{\epsilon}^* > \omega(\Phi_{\epsilon})$ , for sufficiently small  $\epsilon > 0$ . Note that the positive  $\omega$ -periodic function  $v^{\epsilon}(t)$  is bounded on R, and

$$
||e^{-\lambda_{\epsilon}^{*}(t-r)}\Phi_{\epsilon}(t,r)|| \leq M_{\epsilon}e^{(\omega(\Phi_{\epsilon})-\lambda_{\epsilon}^{*})(t-r)}, \ \forall t \geq r, \ r \in \mathbb{R},
$$

for some number  $M_{\epsilon} > 0$ . Letting  $r \to -\infty$  in [\(2.10\)](#page-7-0), we then have

$$
v^{\epsilon}(t) = \int_{-\infty}^{t} e^{-\lambda_{\epsilon}^{*}(t-s)} \Phi_{\epsilon}(t,s) F_{\epsilon}(s) E_{\lambda_{\epsilon}^{*}} v_{s}^{\epsilon} ds = [L_{\lambda_{\epsilon}^{*}}^{\epsilon} v^{\epsilon}](t), \ \forall t \in \mathbb{R},
$$

that is,  $L_{\lambda_{\epsilon}}^{\epsilon}v^{\epsilon} = v^{\epsilon}$ . Since  $L_{\lambda_{\epsilon}}^{\epsilon}$  is compact and strongly positive, the Krein–Rutman theorem implies that  $r(L_{\lambda_{\epsilon}}^{\epsilon}) = 1$  for sufficiently small  $\epsilon > 0$ .

In view of  $\lambda^* > \omega(\Phi)$ , we can fix a small number  $\delta > 0$  such that  $\lambda^* - \delta > \omega(\Phi)$ . Since  $\lim_{\epsilon \to 0^+} \lambda_{\epsilon}^* = \lambda^*$  and  $\lim_{\epsilon \to 0^+} \omega(\Phi_{\epsilon}) = \omega(\Phi)$ , there is a small number  $\epsilon_0 > 0$  such that  $\omega(\Phi) - \lambda^* + \delta + \epsilon_0 M_0 \|E\| < 0$  and

$$
\lambda_{\epsilon}^* \in [\lambda^* - \delta, \lambda^* + \delta], \quad \lambda^* - \delta > \omega(\Phi_{\epsilon}), \quad \forall \epsilon \in [0, \epsilon_0].
$$

Recall that  $c = \epsilon M_0 ||E||$ . Let

$$
A_{\epsilon} := \sup_{0 \le t \le \omega} \|F_{\epsilon}(t)\|, \qquad B_{\epsilon} := \sup_{0 \le t \le \omega} \|F_{\epsilon}(t) - F(t)\|.
$$

By virtue of Lemma [2.2](#page-4-1) and the fact that  $\|\Phi(t, t - s)\| \leq M_0 e^{\omega(\Phi)s}$ , it easily follows that for all  $\epsilon \in [0, \epsilon_0]$  and  $\lambda \in [\lambda^* - \delta, \lambda^* + \delta]$ , there holds

$$
||L_{\lambda}^{\epsilon} - L_{\lambda}|| \leq \int_{0}^{\infty} e^{-\lambda s} \left( cM_{0} s e^{(\omega(\Phi) + c)s} A_{\epsilon} + M_{0} e^{\omega(\Phi)s} B_{\epsilon} \right) ||E_{\lambda}|| ds
$$
  
\n
$$
= ||E_{\lambda}|| \int_{0}^{\infty} \left( cM_{0} s e^{(\omega(\Phi) - \lambda + c)s} A_{\epsilon} + B_{\epsilon} M_{0} e^{(\omega(\Phi) - \lambda)s} \right) ds
$$
  
\n
$$
= \frac{cM_{0} ||E_{\lambda}|| A_{\epsilon}}{(\omega(\Phi) - \lambda + c)^{2}} + \frac{M_{0} ||E_{\lambda}|| B_{\epsilon}}{\omega(\Phi) - \lambda}
$$
  
\n
$$
\leq \frac{\epsilon M_{0}^{2} ||E|| \cdot ||E_{\lambda}|| (\sup_{0 \leq t \leq \omega} ||F(t)|| + \epsilon)}{(\omega(\Phi) - \lambda + \epsilon M_{0} ||E||)^{2}} + \frac{\epsilon M_{0} ||E_{\lambda}||}{\omega(\Phi) - \lambda}.
$$

This implies that  $\lim_{\epsilon \to 0^+} ||L_\lambda^{\epsilon} - L_\lambda|| = 0$  for each  $\lambda \in [\lambda^* - \delta, \lambda^* + \delta]$ , and hence,

$$
\lim_{\epsilon \to 0^+} r(L_\lambda^\epsilon) = r(L_\lambda) = \mu(\lambda), \quad \forall \lambda \in [\lambda^* - \delta, \lambda^* + \delta].
$$

Let  $\epsilon_n = \frac{1}{n}$  and  $\mu_n(\lambda) = r(L_\lambda^{\epsilon_n})$ . By Proposition [2.1,](#page-5-0)  $\mu(\lambda)$  and  $\mu_n(\lambda)$  are continuous on  $[\lambda^* - \delta, \lambda^* + \delta]$ . Since  $L_\lambda^{\epsilon_{n+1}} v \leq L_\lambda^{\epsilon_n} v$  for all  $v \in C_\omega^+$ , it follows that  $\mu_n(\lambda)$  is a nonincreasing sequence of functions. Thus, Dini's theorem implies that  $\lim_{n\to\infty} \mu_n(\lambda) = \mu(\lambda)$  uniformly for  $\lambda \in [\lambda^* - \delta, \lambda^* + \delta]$ . Since

$$
|\mu_n(\lambda_{\epsilon_n}^*) - \mu(\lambda^*)| \leq |\mu_n(\lambda_{\epsilon_n}^*) - \mu(\lambda_{\epsilon_n}^*)| + |\mu(\lambda_{\epsilon_n}^*) - \mu(\lambda^*)|,
$$

we obtain  $\lim_{n\to\infty}\mu_n(\lambda_{\epsilon_n}^*)=\mu(\lambda^*)$ . On the other hand, the conclusion in the last paragraph implies that  $\mu_n(\lambda_{\epsilon_n}^*) = r(L_{\lambda_{\epsilon_n}^*}^{\epsilon_n}) = 1$  for sufficiently large *n*. Letting  $n \to \infty$  in this equality, we then have  $\mu(\lambda^*) = 1$ .

Now we are are ready to prove that  $R_0$  is a threshold value for the stability of the zero solution for periodic system [\(2.1\)](#page-2-0). Recall that  $U(\omega, 0)$  is the Poincaré (period) map of system [\(2.1\)](#page-2-0) on *C*.

<span id="page-8-0"></span>**Theorem 2.1** *The following statements are valid:*

- *(i)*  $R_0 = 1$  *if and only if*  $r(U(\omega, 0)) = 1$ *.*
- *(ii)*  $R_0 > 1$  *if and only if*  $r(U(\omega, 0)) > 1$ *.*
- (*iii*)  $R_0 < 1$  *if and only if*  $r(U(\omega, 0)) < 1$ *.*

*Thus,*  $R_0 - 1$  *has the same sign as*  $r(U(\omega, 0)) - 1$ .

*Proof* In view of  $\omega(\Phi) = \frac{\ln r(\Phi(\omega,0))}{\omega} < 0$ , we have  $r(\Phi(\omega,0)) < 1$ .

(i) (a) If  $R_0 = 1$ , then  $\mu(0) = 1$ . By the proof of Proposition [2.1](#page-5-0) (ii), it follows that  $e^{0\omega} = 1$  is an eigenvalue of  $U(\omega, 0)$ , and hence,  $r(U(\omega, 0)) \ge 1 > r(\Phi(\omega, 0))$ . Thus, Proposition [2.2](#page-6-2) implies that  $\mu(\lambda^*) = 1$ . By Proposition [2.1](#page-5-0) (ii), we further obtain  $\lambda^* = 0$ , that is,  $r(U(\omega, 0)) = 1$ . (b) If  $r(U(\omega, 0)) = 1$ , then  $\lambda^* = 0$ . Since  $r(\Phi(\omega, 0)) < 1$ , Proposition [2.2](#page-6-2) implies that  $\mu(0) = 1$ , that is,  $R_0 = 1$ .

(ii) (a) If  $R_0 > 1$ , then  $\mu(0) > 1$ . Since  $\mu(\lambda)$  is continuous on  $(\omega(\Phi), \infty)$  and  $\mu(\infty) =$ 0 (see Proposition [2.1](#page-5-0) (i)), there exists  $\lambda_0 > 0$  such that  $\mu(\lambda_0) = 1$ . By the proof of Proposition [2.1](#page-5-0) (ii), we see that  $e^{\lambda_0 \omega}$  is an eigenvalue of  $U(\omega, 0)$ , and hence,  $r(U(\omega, 0)) \ge$  $e^{\lambda_0 \omega} > 1$ . (b) If  $r(U(\omega, 0)) > 1$ , then  $\lambda^* > 0$ . Since  $r(\Phi(\omega, 0)) < 1$ , it follows from Proposition [2.2](#page-6-2) that  $\mu(\lambda^*) = 1$ , and hence,  $R_0 = \mu(0) \ge \mu(\lambda^*) = 1$ . But Proposition [2.1](#page-5-0) (ii) implies that  $R_0 = \mu(0) \neq 1$ . Thus, we must have  $R_0 > 1$ .

Clearly, statement (iii) is a straightforward consequence of the conclusions (i) and (ii) above.  $\Box$ 

<span id="page-8-2"></span>For any given  $\lambda \in (0, \infty)$ , we consider the following linear and periodic system:

$$
\frac{du(t)}{dt} = \frac{1}{\lambda}F(t)u_t - V(t)u(t), \quad t \ge 0.
$$
 (2.11)

<span id="page-8-1"></span>Let  $U(t, s, \lambda)$   $(t \geq s)$  be the evolution operators on *C* associated with system [\(2.11\)](#page-8-2). Then we have the following result.

**Theorem 2.2** *If*  $R_0 > 0$ *, then*  $\lambda = R_0$  *is the unique solution of*  $r(U(\omega, 0, \lambda)) = 1$ *.* 

*Proof* By replacing  $F(t)$  with  $\frac{1}{\lambda}F(t)$ , we can define the basic reproduction ratio,  $R(\lambda)$ , for system [\(2.11\)](#page-8-2). It then follows that  $R(\lambda) = r\left(\frac{1}{\lambda}L\right) = \frac{1}{\lambda}R_0$ . By Theorem [2.1,](#page-8-0) we have

$$
sign(R(\lambda) - 1) = sign(r(U(\omega, 0, \lambda)) - 1), \quad \forall \lambda \in (0, \infty).
$$

Letting  $\lambda = R_0 > 0$  in the above equation, we then obtain  $r(U(\omega, 0, R_0)) = 1$ .

It remains to prove that  $r(U(\omega, 0, \lambda)) = 1$  has at most one positive solution for  $\lambda$ . Since *F*(*t*) is a positive operator and  $-V(t)$  is cooperative, the comparison theorem (see [\[19,](#page-15-15) Theorem 5.1.1]) implies that

$$
U(\omega, 0, \lambda_1)\phi \ge U(\omega, 0, \lambda_2)\phi, \quad \forall 0 < \lambda_1 \le \lambda_2, \ \phi \in C^+.
$$

Note that each  $U(\omega, 0, \lambda)$  is a positive and bounded linear operator on *C*. It then fol-lows from [\[4](#page-14-5), Theorem 1.1] that  $r(U(\omega, 0, \lambda))$  is a nonincreasing function of  $\lambda$  on  $(0, \infty)$ . Assume, by contradiction, that  $r(U(\omega, 0, \lambda)) = 1$  has two positive solutions  $\lambda_1 < \lambda_2$ . Then  $r(U(\omega, 0, \lambda)) = 1$ ,  $\forall \lambda \in [\lambda_1, \lambda_2]$ . We choose an integer  $n_0 > 0$  such that  $n_0 \omega > \tau$ . In view of [\[11,](#page-15-14) Theorem 3.6.1], each operator  $U(n_0\omega, 0, \lambda)$  is compact on *C*. Let  $\lambda \in [\lambda_1, \lambda_2]$  be given. Since

$$
r(U(n_0\omega, 0, \lambda)) = r((U(\omega, 0, \lambda))^{n_0}) = (r(U(\omega, 0, \lambda)))^{n_0} = 1 > 0,
$$

the Krein–Rutman theorem implies that 1 is an eigenvalue of  $U(n_0\omega, 0, \lambda)$  with an eigenvector  $\phi^* \in C^+ \setminus \{0\}$ . Since  $U(n_0\omega, 0, \lambda)\phi^* = \phi^*$ , it follows that  $u(t) := [U(t, 0, \lambda)\phi^*](0)$ is an  $n_0\omega$ -periodic solution of system [\(2.11\)](#page-8-2). By the constant-variation formula, we have

$$
u(t) = \Phi(t, r)u(r) + \int_r^t \Phi(t, s)\frac{1}{\lambda}F(s)u_s ds, \quad \forall t \ge r, r \in \mathbb{R}.
$$
 (2.12)

<span id="page-9-1"></span>Note that  $\|\Phi(t, s)\| \leq M_0 e^{\omega(\Phi)(t-s)}$ ,  $\forall t \geq s, s \in \mathbb{R}$ , for some  $M_0 > 0$ . Since  $\omega(\Phi) < 0$ and  $u(t)$  is bounded on R, leting  $r \to -\infty$  in [\(2.12\)](#page-9-1), we further obtain

$$
u(t) = \int_{-\infty}^{t} \Phi(t, s) \frac{1}{\lambda} F(s) u_s ds, \quad \forall t \in \mathbb{R},
$$

and hence,  $Lu = \lambda u$ . Since *L* also defines a compact linear operator on  $C_{n_0\omega}$  (see Lemma [2.1\)](#page-4-2), it follows that  $\lambda$  is an eigenvalue of *L* on  $C_{n_0\omega}$ . Thus, any  $\lambda \in [\lambda_1, \lambda_2]$  is an eigenvalue of *L* on  $C_{n_0\omega}$ , which is impossible since the compact linear operator *L* on  $C_{n_0\omega}$  has only countablely many eigenvalues.  $\Box$ 

For any given  $F \in \mathcal{L}(C, \mathbb{R}^m)$ , we define  $\hat{F} \in \mathcal{L}(\mathbb{R}^m, \mathbb{R}^m)$  by

$$
\hat{F}u = F(\hat{u}), \ \forall u \in \mathbb{R}^m,
$$

where  $\hat{u}(\theta) = u$ ,  $\forall \theta \in [-\tau, 0]$ . Clearly,  $\hat{F}$  can be regarded as an  $m \times m$  matrix. Then we have the following result.

<span id="page-9-0"></span>**Corollary 2.1** *Let*  $F(t) \equiv F \in \mathcal{L}(C, \mathbb{R}^m)$  *and*  $V(t) \equiv V$ *. Then*  $R_0 = r(V^{-1}\hat{F}) =$  $r(FV^{-1})$ .

*Proof* Clearly,  $r(V^{-1}\hat{F}) = r(\hat{F}V^{-1})$ . Without loss of generality, we may assume that  $r(V^{-1}\hat{F}) > 0$  and for all  $\lambda > 0$ ,  $U(t, 0, \lambda)$  is eventually strongly positive on *C* ( see [\[19,](#page-15-15) Section 5.3]). Otherwise, we can choose appropriate small perturbations  $F_{\epsilon}$  and  $V_{\epsilon}$ instead of *F* and *V*, respectively, and then use a limiting argument as  $\epsilon \to 0$ . In view of  $V^{-1} = \int_0^\infty e^{-Vs} ds$  and  $\Phi(t, s) = e^{-V(t-s)}$ , it easily follows that

$$
Lv = V^{-1}\hat{F}v, \quad \forall v \in \mathbb{R}^m.
$$

Note that  $r(V^{-1}\hat{F})$  is an eigenvalue of  $V^{-1}\hat{F}$  with an eigenvector  $v^* \in \mathbb{R}^m_+ \setminus \{0\}$ . Then  $r_0 := r(V^{-1}\hat{F})$  is also an eigenvalue of *L*, and hence,  $R_0 > 0$ . Since  $V^{-1}\hat{F}v^* = r_0v^*$ , we have  $\frac{1}{r_0} \hat{F} v^* - V v^* = 0$ , which implies that  $u(t) = v^*$  is a constant solution to

$$
\frac{du(t)}{dt} = \frac{1}{r_0}Fu_t - Vu(t).
$$

Thus,  $U(t, 0, r_0)v^* = v^*$ ,  $\forall t \geq 0$ . We fix a large integer  $n_0 > 0$  such that  $U(n_0\omega, 0, r_0)$  is compact and strongly positive. By the Krein–Rutman theorem, we then obtain  $r(U(n_0\omega, 0, r_0)) = 1$ . Since

$$
r(U(n_0\omega, 0, r_0)) = r((U(\omega, 0, r_0))^{n_0}) = (r(U(\omega, 0, r_0)))^{n_0},
$$

it follows that  $r(U(\omega, 0, r_0)) = 1$ . Now Theorem [2.2](#page-8-1) implies that  $R_0 = r_0$ .

In the case where  $\tau = 0$ , Theorems [2.1](#page-8-0) and [2.2](#page-8-1) reduce to Theorems 2.2 and 2.1 (ii) of [\[24\]](#page-15-2), respectively, and Corollary [2.1](#page-9-0) is consistent with the formula of *R*<sup>0</sup> given in [\[23\]](#page-15-1). More recently, the basic reproduction number was addressed in [\[28\]](#page-15-18) for linear autonomous systems with discrete delays:

$$
\frac{dI(t)}{dt} = F_1 I(t - \tau_1) + F_2 I(t - \tau_2) - VI(t),
$$

where  $F_1$  and  $F_2$  are nonnegative matrices and  $-V$  is a cooperative matrix. Taking  $F(\phi)$  =  $F_1\phi(-\tau_1) + F_2\phi(-\tau_2)$  and  $\tau = \max{\lbrace \tau_1, \tau_2 \rbrace}$ , we have  $\hat{F} = F_1 + F_2$ . Thus, Corollary [2.1](#page-9-0) implies that  $R_0 = r((F_1 + F_2)V^{-1})$ , which is the same as the formula obtained in [\[28\]](#page-15-18). Clearly, Corollary [2.1](#page-9-0) also applies to more general linear autonomous systems with distributed delays.

<span id="page-10-0"></span>*Remark 2.1* The theory of basic reproduction ratio in this section can be extended to abstract periodic linear systems with time delay if we replace R*<sup>m</sup>* with an ordered Banach space *E* and assume that each  $-V(t)$  is a linear operator such that the linear equation  $\frac{du}{dt} = -V(t)u$  generates a positive evolution operator  $\Phi(t, s)$  on *E*. Thus, one can apply the generalized theory to periodic and time-delayed reaction-diffusion population models. For example, letting  $\Omega$  be a bounded domain with smooth boundary,  $E = C(\overline{\Omega}, \mathbb{R}^m)$  and  $-V(t)u = D(t)\Delta u - W(t)u$ , we can consider the following periodic linear system:

$$
\frac{\partial u}{\partial t} = D(t)\Delta u + F(t)u_t - W(t)u,
$$

subject to the Neumann boundary condition. Here  $\Delta u = (\Delta u_1, \dots, \Delta u_m)^T$ ,  $[D(t)](x) =$  $diag(d_1(t, x), \ldots, d_m(t, x))$  with  $d_i(t, x) > 0$  or  $d_i(t, x) \equiv 0$ , and for each  $t \in \mathbb{R}$ ,  $F(t) \in$  $\mathcal{L}(C([- \tau, 0], E), E)$  and  $-[W(t)](x)$  is an *m* × *m* cooperative matrix function of  $x \in \overline{\Omega}$ .

#### <span id="page-10-1"></span>**3 An Application**

We consider a continuous-time SEIR model of a disease transmission. Let  $S(t)$ ,  $E(t)$ ,  $I(t)$ and  $R(t)$  be the total numbers at time  $t$  of the susceptible, exposed, infective, and recovered (or removed) populations, respectively. For simplicity, we assume that the latent period of the disease is  $\tau$ , and the incidence rate function  $f(t, S, I)$  depends on time t and variables *S* and *I*. Let  $\mu(t)$  be the natural death rate of the population. It then follows that the rate of entry into the infective class from the exposed one at time *t* is

$$
e^{-\int_{t-\tau}^t \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)).
$$

As discussed in  $[20]$  $[20]$ ,  $E(t)$  can be represented as

$$
E(t) = \int_{t-\tau}^t e^{-\int_s^t \mu(r)dr} f(s, S(s), I(s))ds.
$$

<span id="page-10-2"></span>Thus, we obtain the following nonautonomous SEIR model:

$$
\frac{dS(t)}{dt} = \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t),
$$
  
\n
$$
E(t) = \int_{t-\tau}^{t} e^{-\int_{s}^{t} \mu(r)dr} f(s, S(s), I(s))ds,
$$
  
\n
$$
\frac{dI(t)}{dt} = e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)) - (\mu(t) + d(t) + \gamma(t))I(t),
$$

 $\circled{2}$  Springer

$$
\frac{dR(t)}{dt} = \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t).
$$
\n(3.1)

Here  $\Lambda(t)$  is the recruitment rate,  $d(t)$  is the disease-induced death rate,  $\gamma(t)$  is the recovery rate, and  $\alpha(t)$  is the loss of immunity rate.

<span id="page-11-0"></span>According to [\[5](#page-14-6)], we need to impose the following compatibility condition:

$$
E(0) = \int_{-\tau}^{0} e^{-\int_{s}^{0} \mu(r) dr} f(s, S(s), I(s)) ds.
$$
 (3.2)

It is easy to verify that

$$
\frac{dE(t)}{dt} = f(t, S(t), I(t)) - e^{-\int_{t-\tau}^{t} \mu(r) dr} f(t-\tau, S(t-\tau), I(t-\tau)) - \mu(t)E(t).
$$

<span id="page-11-1"></span>Thus, model [\(3.1\)](#page-10-2) reduces to the following nonautonomous functional differential system:

$$
\frac{dS(t)}{dt} = \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t),
$$
\n
$$
\frac{dE(t)}{dt} = f(t, S(t), I(t)) - e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t - \tau, S(t - \tau), I(t - \tau)) - \mu(t)E(t),
$$
\n
$$
\frac{dI(t)}{dt} = e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t - \tau, S(t - \tau), I(t - \tau)) - (\mu(t) + d(t) + \gamma(t))I(t),
$$
\n
$$
\frac{dR(t)}{dt} = \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t),
$$
\n(3.3)

subject to condition  $(3.2)$ .

We assume that  $f(t, S, I)$  and all these time-dependent coefficients are  $\omega$ -periodic in *t* for some real number  $\omega > 0$ . It is then easy to see that the function

$$
p(t) := e^{-\int_{t-\tau}^t \mu(r) dr}
$$

is also  $\omega$ -periodic, and hence, model [\(3.3\)](#page-11-1) is an  $\omega$ -periodic and time-delayed system. To study the evolution dynamics of system [\(3.3\)](#page-11-1), we make the following assumptions.

- (A1)  $\Lambda(t)$ ,  $\mu(t)$ ,  $\alpha(t)$ ,  $d(t)$ , and  $\gamma(t)$  are all non-negative and continuous functions with  $\Lambda(t) > 0$ ,  $\int_0^{\omega} \mu(t) dt > 0$ , and  $\int_0^{\omega} \gamma(t) dt > 0$ .
- (A2)  $f(t, S, I)$  is a  $C<sup>1</sup>$ -function with the following properties:
	- (i)  $f(t, S, 0) \equiv 0$ ,  $f(t, 0, I) \equiv 0$ , and  $\frac{\partial f(t, S, 0)}{\partial I}$  are positive and non-decreasing for all  $S > 0$ .
	- $\frac{\partial f(t, S, I)}{\partial S} \ge 0$  and  $f(t, S, I) \le \frac{\partial f(t, S, 0)}{\partial I} I$  for all  $(t, S, I) \in \mathbb{R} \times \mathbb{R}^2_+.$

A prototypical example for incidence function is  $f(t, S, I) = \frac{\beta(t)SI}{1+c(t)I}$  with  $c(t) \ge 0$ . For more general time-independent incidence functions, we refer to  $[13]$  and references therein.

<span id="page-11-2"></span>By virtue of (A1), we see that the scalar linear periodic equation

$$
\frac{dS(t)}{dt} = \Lambda(t) - \mu(t)S(t)
$$
\n(3.4)

<span id="page-11-3"></span>has a unique positive  $\omega$ -periodic solution  $S^*(t)$ , which is globally stable in R. Linearizing system [\(3.3\)](#page-11-1) at its disease-free periodic solution  $(S^*(t), 0, 0, 0)$ , we then obtain the following periodic linear equation for the infective variable *I*:

$$
\frac{dI(t)}{dt} = a(t)I(t-\tau) - b(t)I(t),\tag{3.5}
$$

where

$$
a(t) = p(t) \frac{\partial f(t - \tau, S^*(t - \tau), 0)}{\partial I}, \qquad b(t) = \mu(t) + d(t) + \gamma(t).
$$

Following the procedure in Sect. [2,](#page-1-0) we take  $m = 1$ ,  $F(t)\phi = a(t)\phi(-\tau)$ , and  $V(t) = b(t)$ . It then easily follows that

$$
\Phi(t,s) = e^{-\int_s^t b(r)dr}, \quad \forall t \geq s, \ s \in \mathbb{R},
$$

and

$$
[Lv](t) = \int_0^\infty \Phi(t, t - s)F(t - s)v(t - s + \cdot)ds
$$
  
= 
$$
\int_0^\infty \Phi(t, t - s)a(t - s)v(t - s - \tau)ds
$$
  
= 
$$
\int_t^\infty \Phi(t, t - s + \tau)a(t - s + \tau)v(t - s)ds
$$
  
= 
$$
\int_0^\infty K(t, s)v(t - s)ds, \quad \forall t \in \mathbb{R}, v \in C_\omega,
$$

where

$$
K(t,s) = \begin{cases} \Phi(t, t - s + \tau)a(t - s + \tau), & \text{if } s \ge \tau \\ 0, & \text{if } s < \tau. \end{cases}
$$

According to the definition in Sect. [2,](#page-1-0) we have  $R_0 = r(L)$ .

<span id="page-12-0"></span>Since the *S*, *I* and *R* equations in model [\(3.3\)](#page-11-1) do not depend on variable *E*, it suffices to study the following  $\omega$ -periodic system with time delay:

$$
\frac{dS(t)}{dt} = \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t),
$$
  
\n
$$
\frac{dI(t)}{dt} = p(t)f(t - \tau, S(t - \tau), I(t - \tau)) - (\mu(t) + d(t) + \gamma(t))I(t),
$$
  
\n
$$
\frac{dR(t)}{dt} = \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t).
$$
\n(3.6)

Let  $X = C([- \tau, 0], \mathbb{R}^3_+).$  By the standard theory of functional differential equations (see, e.g., [\[11\]](#page-15-14)), system [\(3.6\)](#page-12-0) admits a unique nonnegative solution  $v(t, \phi) = (S(t), I(t), R(t))$ satisfying  $v_0(\phi) = \phi \in X$ . Define

$$
D := \left\{ \psi \in C \Big( [-\tau, 0], \mathbb{R}^4_+ \Big) : \psi_2(0) = \int_{-\tau}^0 e^{-\int_s^0 \mu(r) dr} f(s, \psi_1(s), \psi_3(s)) ds \right\}.
$$

It then easily follows that for any  $\psi \in D$ , system [\(3.3\)](#page-11-1) has a unique nonnegative solution  $u(t, \psi) = (S(t), E(t), I(t), R(t))$  satisfying  $u_0(\psi) = \psi$ . Let  $N(t) = S(t) + E(t) + I(t) + I(t)$ *R*(*t*). Then we have

$$
\frac{dN(t)}{dt} = \Lambda(t) - \mu(t)N(t) - d(t)I(t) \le \Lambda(t) - \mu(t)N(t), \quad t \ge 0.
$$
 (3.7)

<span id="page-12-1"></span>Thus, the global stability of  $S^*(t)$  for [\(3.4\)](#page-11-2), together with the comparison argument, implies that solutions of system  $(3.3)$  with initial data in *D*, and hence  $(3.6)$  in *X*, exist globally on  $[0, \infty)$  and are ultimately bounded.

Let  $X_0 = \{\phi = (\phi_1, \phi_2, \phi_3) \in X : \phi_2(0) > 0\}$ . The subsequent result shows that  $R_0$ serves as a threshold value for the global extinction and uniform persistence of the disease.

**Theorem 3.1** *Let (A1) and (A2) hold. Then the following statements are valid:*

- *(i)* If  $R_0 < 1$ , then the disease-free periodic solution  $(S^*(t), 0, 0)$  is globally attractive for *system* [\(3.6\)](#page-12-0) *in X.*
- *(ii)* If  $R_0 > 1$ , then system [\(3.6\)](#page-12-0) admits a positive  $\omega$ -periodic solution  $(\bar{S}(t), \bar{I}(t), \bar{R}(t))$ , *and there exists a real number*  $\eta > 0$  *such that the solution u(t,*  $\phi$ *)* = (*S(t), I(t), R(t)*) *satisfies*  $\liminf_{t\to\infty} I(t) \geq \eta$  *for any*  $\phi \in X_0$ *.*

*Proof* Let  $P(t)$  be the solution maps of the scalar linear equation [\(3.5\)](#page-11-3) on  $Y := C([-t, 0], \mathbb{R})$ , that is,  $P(t)\phi = w_t(\psi)$ ,  $t > 0$ , where  $w(t, \psi)$  is the unique solution of [\(3.5\)](#page-11-3) satisfying  $w_0 =$  $\psi \in Y$ . Then  $P := P(\omega)$  is the Poincaré (period) map associated with system [\(3.5\)](#page-11-3). In view of Theorem [2.1,](#page-8-0) we have  $sign(R_0 - 1) = sign(r(P) - 1)$ . Since  $p(t) \frac{\partial f(t-\tau, S^*(t-\tau),0)}{\partial I} > 0$ , is a fillowing from [\[11](#page-15-14), Theorem 3.6.1] and [\[19](#page-15-15), Lemma 5.3.2] that for each  $t \ge 2\tau$ , the linear operator  $P(t)$  is compact and strongly positive on *Y*. Choose an integer  $n_0 > 0$  such that  $n_0 \omega > 2\tau$ . Since  $P^{n_0} = P(n_0 \omega)$ , [\[14,](#page-15-16) Lemma 3.1] implies that  $r(P)$  is a simple eigenvalue of *P* having a strongly positive eigenvector, and the modulus of any other eigenvalue is less than  $r(P)$ . Let  $\mu = \frac{\ln r(P)}{\omega}$ . By the proof of [\[29](#page-15-17), Proposition 2.1], it then follows that there is positive  $\omega$ -periodic function  $v(t)$  such that  $u(t) = e^{\mu t}v(t)$  is a positive solution of [\(3.5\)](#page-11-3).

In the case where  $R_0 < 1$ , we have  $r(P) < 1$ . Let  $P_\epsilon$  be the Poincaré map of the following perturbed linear periodic equation

$$
\frac{dI(t)}{dt} = p(t)\frac{\partial f(t-\tau, S^*(t-\tau) + \epsilon, 0)}{\partial I}I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t). \tag{3.8}
$$

<span id="page-13-0"></span>Since  $\lim_{\epsilon \to 0} r(P_{\epsilon}) = r(P) < 1$ , we can fix a sufficiently small number  $\epsilon > 0$  such that  $r(P_{\epsilon})$  < 1. As discussed in the last paragraph, there is positive  $\omega$ -periodic function  $v_{\epsilon}(t)$ such that  $u_{\epsilon}(t) = e^{\mu_{\epsilon}t}v_{\epsilon}(t)$  is a positive solution of [\(3.8\)](#page-13-0), where  $\mu_{\epsilon} = \frac{\ln r(P_{\epsilon})}{\omega} < 0$ . For any given  $\phi \in X$ , let  $v(t, \phi) = (S(t), I(t), R(t))$ . In view of [\(3.7\)](#page-12-1) and the global stability of  $S^*(t)$  for [\(3.4\)](#page-11-2), it follows that there exists a sufficiently large integer  $n_1 > 0$  such that  $n_1\omega \geq \tau$  and  $S(t) \leq S^*(t) + \epsilon$ ,  $\forall t \geq n_1\omega - \tau$ . By assumption (A2), we then have

$$
\frac{dI(t)}{dt} \le p(t) \frac{\partial f(t-\tau, S^*(t-\tau) + \epsilon, 0)}{\partial I} I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t)
$$

for all  $t > n_1\omega$ . Choose a sufficiently large number  $K > 0$  such that  $I(t) \leq K u_{\epsilon}(t)$ ,  $\forall t \in$ [*n*1ω−τ, *n*1ω]. Thus, the comparison theorem for delay differential equations ([\[19,](#page-15-15) Theorem 5.1.1]) implies that

$$
I(t) \leq Ku_{\epsilon}(t) = Ke^{\mu_{\epsilon}t}v_{\epsilon}(t), \quad \forall t \geq n_1\omega,
$$

and hence,  $\lim_{t\to\infty} I(t) = 0$ . By using the chain transitive sets arguments (see, e.g., [\[15,](#page-15-21) Theorem 4.1(a)]), it easily follows that  $\lim_{t\to\infty} R(t) = 0$  and  $\lim_{t\to\infty} (S(t) - S^*(t)) = 0$ .

In the case where  $R_0 > 1$ , we have  $r(P) > 1$ . Let  $Q(t)\phi = v_t(\phi)$ ,  $\forall \phi \in X$ , and  $Q = Q(\omega)$ . Clearly,  $\{Q(t)\}_{t>0}$  is an  $\omega$ -periodic semiflow on *X* (see [\[30\]](#page-15-13)), and  $Q^n =$  $Q(n\omega)$ ,  $\forall n \geq 0$ . Let  $M_\delta$  be the Poincaré map of the following perturbed linear periodic equation

$$
\frac{dI(t)}{dt} = p(t) \left( \frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I} - \delta \right) I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t).
$$

Since  $\lim_{\delta \to 0} r(M_\delta) = r(P) > 1$ , we can fix a small number  $\delta > 0$  such that  $r(M_\delta) > 1$ . It then follows that there is a small number  $\eta_0 > 0$  such that

$$
f(t-\tau, S^*(t-\tau)-\eta_0, I) \ge \left(\frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I} - \delta\right)I, \ \forall I \in [0, \eta_0].
$$

Note that (A2) implies that  $f(t, S, I)$  is non-decreasing in *S*. Let  $M_1 = (S^*(0), 0, 0)$ . Then  $Q(M_1) = M_1$ . By a contradiction argument similar to that in the proof of [\[29,](#page-15-17) Lemma 3.2], we can further prove the following claim.

*Claim.*  $\limsup_{n\to\infty} ||Q^n(\phi) - M_1|| \geq \eta_0, \ \forall \phi \in X_0.$ This implies that *M*<sub>1</sub> is an isolated invariant set for *Q* in *X* and  $W<sup>s</sup>(M<sub>1</sub>) \cap X<sub>0</sub> = \emptyset$ , where  $W<sup>s</sup>(M<sub>1</sub>)$  is the stable set of *M*<sub>1</sub> for *Q*. Set ∂ *X*<sub>0</sub> = *X* \ *X*<sub>0</sub> and

$$
M_{\partial} = \{ \phi \in \partial X_0 : \ Q^n(\phi) \in \partial X_0, \ \forall n \ge 0 \}.
$$

Since

$$
\frac{dI(t)}{dt} \geq -(\mu(t) + d(t) + \gamma(t))I(t), \ \forall t \geq 0,
$$

it is easy to see that if  $I(t_0) > 0$  for some  $t_0 \ge 0$ , then  $I(t) > 0$  for all  $t \ge t_0$ . This property implies that  $I(t) = 0$ ,  $\forall t \geq 0$ , whenever  $\phi \in M_{\partial}$ . It then follows that  $\omega(\phi) = M_1$  for any  $\phi \in M_{\partial}$ , and  $M_1$  cannot form a cycle for *Q* in  $\partial X_0$ . By the acyclicity theorem on uniform persistence for maps (see, e.g., [\[30](#page-15-13), Theorem 1.3.1 and Remark 1.3.1]),  $Q: X \rightarrow X$  is uniformly persistent with respect to  $X_0$ . Thus, [\[30,](#page-15-13) Theorem 3.1.1] implies that the periodic semiflow  $Q(t)$ :  $X \to X$  is also uniformly persistent with respect to  $X_0$ . Note that  $\gamma(t) \neq 0$ and  $f(t, 0, I) \equiv 0$ . By similar arguments to those in the proof of [\[15](#page-15-21), Theorem 4.1(b)], we then obtain the existence of a positive  $\omega$ -periodic solution and the desired persistence for system  $(3.6)$ .

To finish this paper, we remark that unlike in the case of periodic ODEs, it is not easy to use Theorem [2.2](#page-8-1) to compute numerically  $R_0$  for periodic and time-delayed population models. This is because the linear operators  $U(\omega, 0, \lambda)$  are defined on the Banach space  $C([-\tau, 0], \mathbb{R}^m)$ . However, one may employ the orthogonal projection method in the computation of eigenvalues for compact linear operators (see, e.g., [\[6](#page-14-7), Section 3]) to compute  $R_0 = r(L)$ .

**Acknowledgements** The author is very grateful to the anonymous referee for careful reading and valuable comments which led to important improvements of the original manuscript. This research was supported in part by the NSERC of Canada.

#### <span id="page-14-1"></span>**References**

- 1. Bacaër, N., Ait, E.H.: Dads, genealogy with seasonality, the basic reproduction number, and the influenza pandemic. J. Math. Biol. **62**, 741–762 (2011)
- <span id="page-14-2"></span>2. Bacaër, N., Ait, E.H.: Dads, on the biological interpretation of a definition for the parameter  $R_0$  in periodic population models. J. Math. Biol. **65**, 601–621 (2012)
- <span id="page-14-0"></span>3. Bacaër, N., Guernaoui, S.: The epidemic threshold of vector-borne diseases with seasonality. J. Math. Biol. **53**, 421–436 (2006)
- <span id="page-14-5"></span>4. Burlando, L.: Monotonicity of spectral radius for positive operators on ordered Banach spaces. Arch. Math. **56**, 49–57 (1991)
- <span id="page-14-6"></span>5. Busenberg, S., Cooke, K.L.: The effect of integral conditions in certain equations modelling epidemics and population growth. J. Math. Biol. **10**, 13–32 (1980)
- <span id="page-14-7"></span>6. Chatelin, F.: The spectral approximation of linear operators with applications to the computation of eigenelements of differential and integral operators. SIAM Rev. **23**, 495–522 (1981)
- <span id="page-14-3"></span>7. Daners, D., Koch Medina, P.: Abstract evolution equations, periodic problems and applications. Pitman Research Notes in Mathematics Series, vol. 279. Longman Scientific & Technical, Harlow, Wiley, New York (1992)
- <span id="page-14-4"></span>8. Degla, G.: An overview of semi-continuity results on the spectral radius and positivity. J. Math. Anal. Appl. **338**, 101–110 (2008)
- <span id="page-15-0"></span>9. Diekmann, O., Heesterbeek, J.A.P., Metz, J.A.J.: On the definition and the computation of the basic reproduction ratio *R*0 in the models for infectious disease in heterogeneous populations. J. Math. Biol. **28**, 365–382 (1990)
- <span id="page-15-5"></span>10. Guo, Z., Wang, F., Zou, X.: Threshold dynamics of an infective disease model with a fixed latent period and non-local infections. J. Math. Biol. **65**, 1387–1410 (2012)
- <span id="page-15-14"></span>11. Hale, J.K., Verduyn Lunel, S.M.: Introduction to Functional Differential Equations. Springer, New York (1993)
- <span id="page-15-4"></span>12. Inaba, H.: On a new perspective of the basic reproduction number in heterogeneous environments. J. Math. Biol. **65**, 309–348 (2012)
- <span id="page-15-20"></span>13. Korobeinikov, A., Maini, P.K.: Non-linear incidence and stability of infectious disease models. Math. Med. Biol. **22**, 113–128 (2005)
- <span id="page-15-16"></span>14. Liang, X., Zhao, X.-Q.: Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. Commun. Pure Appl. Math. **60**, 1–40 (2007)
- <span id="page-15-21"></span>15. Lou, Y., Zhao, X.-Q.: Threshold dynamics in a time-delayed periodic SIS epidemic model. Discret. Contin. Dyn. Syst. Ser. B **12**, 169–186 (2009)
- <span id="page-15-6"></span>16. Lou, Y., Zhao, X.-Q.: A reaction-diffusion malaria model with incubation period in the vector population. J. Math. Biol. **62**, 543–568 (2011)
- <span id="page-15-7"></span>17. Mckenzie, H.W., Jin, Y., Jacobsen, J., Lewis, M.A.: *R*0 analysis of a spatiotemporal model for a stream population. SIAM J. Appl. Dyn. Syst. **11**, 567–596 (2012)
- <span id="page-15-12"></span>18. Rebelo, C., Margheri, A., Bacaër, N.: Persistence in some periodic epidemic models with infection age or constant periods of infection. Discret. Contin. Dyn. Syst. Ser. B **19**, 1155–1170 (2014)
- <span id="page-15-15"></span>19. Smith, H.L.: Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems, Mathematical Surveys and Monographs 41. American Mathematical Society, Providence (1995)
- <span id="page-15-19"></span>20. Thieme, H.R.: Global asymptotic stability in epidemic models. In: Knobloch, H.W., Schmitt, K., (eds.) Proceedings Equadiff 82, pp. 608–615. Lecture Notes in Mathematics, vol. 1017. Springer, Berlin (1983)
- <span id="page-15-11"></span>21. Thieme, H.R.: Renewal theorems for linear periodic Volterra integral equations. J. Integral Equ. **7**, 253– 277 (1984)
- <span id="page-15-3"></span>22. Thieme, H.R.: Spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity. SIAM J. Appl. Math. **70**, 188–211 (2009)
- <span id="page-15-1"></span>23. van den Driessche, P., Watmough, J.: Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission. Math. Biosci. **180**, 29–48 (2002)
- <span id="page-15-2"></span>24. Wang, W., Zhao, X.-Q.: Threshold dynamics for compartmental epidemic models in periodic environments. J. Dyn. Diff. Equ. **20**, 699–717 (2008)
- <span id="page-15-8"></span>25. Wang, W., Zhao, X.-Q.: A nonlocal and time-delayed reaction-diffusion model of Dengue transmission. SIAM J. Appl. Math. **71**, 147–168 (2011)
- <span id="page-15-9"></span>26. Wang, W., Zhao, X.-Q.: Basic reproduction numbers for reaction–diffusion epidemic models. SIAM J. Appl. Dyn. Syst. **11**, 1652–1673 (2012)
- <span id="page-15-10"></span>27. Wang, B.-G., Zhao, X.-Q.: Basic reproduction ratios for almost periodic compartmental epidemic models. J. Dyn. Differ. Equ. **25**, 535–562 (2013)
- <span id="page-15-18"></span>28. Xiao, Y., Zou, X.: Transmission dynamics for vector-borne diseases in a patchy environment. J. Math. Biol. **69**, 113–146 (2014)
- <span id="page-15-17"></span>29. Xu, D., Zhao, X.-Q.: Dynamics in a periodic competitive model with stage structure. J. Math. Anal. Appl. **311**, 417–438 (2005)
- <span id="page-15-13"></span>30. Zhao, X.-Q.: Dynamical Systems in Population Biology. Springer, New York (2003)