
A Population Model with Periodic Delay

The rhythm of life on earth, occurring on daily or annual scales, is driven by seasonal changes in the environment [348] which regulate various physiological and behavioral processes, as well as the population dynamics of species. Many plant and animal species have demonstrated seasonal population dynamics in response to seasonal environmental changes, in particular, the weather conditions. Mosquito species *Culex pipiens* and *Culex restuans*, main vectors of West Nile virus transmission, are very sensitive to long-term variations in climate and short-term variations in weather [397], in particular, temperature condition affects the rates of immature mosquito development and activity of adults, and precipitation determines the amount and quality of larval habitats. Temperature also affects the host-seeking activity of ticks and their rates from one life stage to the next one, as a result, it is proposed as a statistically significant determinant and possible driver of emergence of the tick in Canada [262]. Seasonal forcing in host and parasite biology also determines the risk of infectious diseases through the following aspects [10]: (a) host social behavior and aggregation; (b) vector population and activity; (c) parasite stages in the environment; (d) timing of reproduction and pulses of susceptible hosts; and (e) host susceptibility and immune defences.

Given the significant roles that seasonal environment factors play in population growth, disease transmission, and other life systems, theoretical models have been formulated to incorporate the seasonality of parameters in phenomenological ways such as those reported in [10]. Many model parameters in ecosystems are influenced by the environmental conditions in a nonlinear way [250], and in previous models, it is well accepted to assume the parameters subject to seasonal factors change periodically. A growing body of literature reported that the developmental duration can be driven by seasonal forcing, and thus be periodic. For example, the developmental duration of mosquito species *Culex pipiens* and *Culex restuans* is affected by temperature conditions. In the transmission cycle of malaria, the extrinsic incubation period (EIP) of the parasite within the mosquito is one of the most critical parameters to

evaluate the disease risk. During EIP, malaria parasites go through various developmental stages and distinct replication cycles before migrating to the salivary glands where they can be transmitted to humans. The speed of this development depends on host, parasite, and environmental factors with estimate order of 10–14 days in areas of high malaria transmission. However, 90% of the female mosquitoes die within 12 days and are therefore unlikely to contribute to malaria transmission. On the other side, the extrinsic incubation period is extremely temperature sensitive [267], and hence, it is pivotal to incorporate this seasonally forced incubation period in the description of malaria transmission. For these two aforementioned scenarios, the developmental durations for immature mosquitoes and incubation period for parasites are periodic functions of time, which brings new challenges into model formulation where careful mathematical derivation and biological justification are needed. The purpose of this chapter is to propose a synthesized mathematical approach to the study of biological systems with seasonal forcing, in particular, with seasonal variations on developmental duration.

In Section 12.1, we use the host-macroparasite interaction as a motivating example to present our approach. The host-parasite interaction has attracted great attention since the pioneering work of Anderson and May [15], with most models aiming to figure out the basic reproduction number R_0 of parasite (measuring “the expected lifetime reproductive output of a new born larva” for macroparasite [250]). Here we develop a theoretical framework to investigate the population dynamics with time-dependent developmental duration for the parasitic nematodes with a direct life cycle and endotherm hosts [250]. This framework can be extended to the population growth, pathogen transmission, and in-host viral dynamics. In Section 12.2, we introduce the basic reproduction ratio R_0 for the model system and establish a threshold-type result on its global dynamics in terms of R_0 . In Section 12.3, we show how to write the next generation operator into the integral form in Posny and Wang [282] so that their numerical method remains applicable to the computation of R_0 for our model system. For reader’s convenience, we also include the algorithm of [282] at the end of this section.

12.1 Model Formulation

Before introducing the whole model system for host-parasite interaction, we investigate a two-stage single population growth scenario as a toy example, in the hope of presenting the modelling idea through a simpler case.

We start with a two-stage model, with population containing first stage $I(t)$ and second stage $M(t)$ defined, respectively, as those of age less than, and greater than, some threshold age $\tau(t)$ (the maturation time for the cohort that matures at time t), which is assumed to be seasonal due to the seasonal variations of weather conditions. That is, at time t , the individuals with age greater (less) than $\tau(t)$ are in the second stage (remaining in the first stage).

Within each age group, all individuals have the same age-independent birth and death rates. Let $\rho(t, a)$ be the population density of age a at time t , then the numbers $I(t)$ and $M(t)$ of individuals in the first and second stages, respectively, are given by

$$I(t) = \int_0^{\tau(t)} \rho(t, a) da \quad \text{and} \quad M(t) = \int_{\tau(t)}^{\infty} \rho(t, a) da.$$

The age density $\rho(t, a)$ satisfies the following McKendrick von-Foerster type equation [77, 400]

$$\frac{\partial \rho(t, a)}{\partial t} + \frac{\partial \rho(t, a)}{\partial a} = -\mu(a, t)\rho(t, a), \tag{12.1}$$

with the age-dependent death rates

$$\mu(a, t) = \mu_1(t) \text{ if } a \leq \tau(t) \quad \text{and} \quad \mu(a, t) = \mu_2(t) \text{ if } a > \tau(t).$$

Taking the derivatives of $I(t)$ and $M(t)$, and using (12.1), we obtain

$$\begin{aligned} \frac{dI(t)}{dt} &= \rho(t, 0) - (1 - \tau'(t))\rho(t, \tau(t)) - \mu_1(t)I(t), \\ \frac{dM(t)}{dt} &= (1 - \tau'(t))\rho(t, \tau(t)) - \mu_2(t)M(t) - \rho(t, \infty). \end{aligned}$$

Since no individual can live forever, $\rho(t, \infty)$ is taken as zero. The term $\rho(t, 0)$ represents the flow in rate to the first stage at time t , supposed to be $\rho(t, 0) = b(t) = B(t, M(t))$, a function of time t and population density $M(t)$. Mathematically, we also assume the delay $\tau(t)$ involved is continuously differentiable in $[0, \infty)$ and bounded away from zero and infinity. To close the system, we calculate $\rho(t, \tau(t))$ in terms of $\rho(t - \tau(t), 0) = b(t - \tau(t)) = B(t - \tau(t), M(t - \tau(t)))$, which is achieved by the technique of integration along characteristics with the aid of the variable $V^s(t) = \rho(t, t - s)$. By direct calculations, we arrive at

$$\frac{d}{dt} V^s(t) = -\mu_1(t)V^s(t)$$

for $t - s \leq \tau(t)$, with $V^s(s) = \rho(s, 0) = b(s)$. It follows that

$$V^s(t) = V^s(s)e^{-\int_s^t \mu_1(\xi) d\xi} = B(s, M(s))e^{-\int_s^t \mu_1(\xi) d\xi}.$$

Setting $s = t - \tau(t)$, we have, for $t \geq \hat{\tau}$ with $\hat{\tau} = \max\{\tau(t)\}$,

$$\rho(t, \tau(t)) = V^{t-\tau(t)}(t) = B(t - \tau(t), M(t - \tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi) d\xi}.$$

Hence, we obtain a closed system to describe two age groups subject to seasonal effects for $t \geq \hat{\tau}$:

$$\begin{aligned} \frac{dI(t)}{dt} &= B(t, M(t)) - (1 - \tau'(t))B(t - \tau(t), M(t - \tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi) d\xi} \\ &\quad - \mu_1(t)I(t), \\ \frac{dM(t)}{dt} &= (1 - \tau'(t))B(t - \tau(t), M(t - \tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi) d\xi} - \mu_2(t)M(t). \end{aligned} \tag{12.2}$$

This model turns out to be a differential system with periodic time delay, which is different from the traditional delay differential models without seasonal effects in the sense that the term $1 - \tau'(t)$ is included in the development rate from the first stage to the next one:

$$(1 - \tau'(t))B(t - \tau(t), M(t - \tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi) d\xi}. \quad (12.3)$$

An alternative approach, more biologically oriented, to describe the population growth of two stages (especially the maturation term (12.3)) is also feasible. The first stage population size $I(t)$ at time t counts all accumulation of individuals born at moment ξ with rate $b(\xi)$ between $t - \tau(t)$ to t but remain alive with the survival probability $e^{-\int_{\xi}^t \mu_1(s) ds}$. Intuitively, the size $I(t)$ depends on the duration of $\tau(t)$ for individuals staying in the first stage. Motivated by these biological inductions, we can represent $I(t)$ by an integral form

$$I(t) = \int_{t-\tau(t)}^t b(\xi)e^{-\int_{\xi}^t \mu_1(s) ds} d\xi.$$

Taking the derivative of $I(t)$, we get the differential equation version of this variable in the first equation of (12.2). The maturation rate should be the birth rate at time $t - \tau(t)$, $b(t - \tau(t))$, multiplied with survival probability to time t , $e^{-\int_{t-\tau(t)}^t \mu_1(s) ds}$, and corrected with the rate of change for $t - \tau(t)$.

In parameterizing the delay $\tau(t)$, the developmental proportion $r(\xi)$ at time ξ is taken into consideration such that the accumulative proportion from $t - \tau(t)$ to t reaches unity when the individual moves to the next stage. Theoretically, we use the following relation to determine $\tau(t)$

$$1 = \int_{t-\tau(t)}^t r(\xi)d\xi, \quad (12.4)$$

where $r(\xi)$ is the time-periodic development proportion at moment ξ . The periodicity of $r(\xi)$ in ξ implies the periodicity of the delay $\tau(t)$ in time variable t . Taking the derivative with respect to t , we have

$$0 = r(t) - (1 - \tau'(t))r(t - \tau(t))$$

from which we obtain

$$1 - \tau'(t) = \frac{r(t)}{r(t - \tau(t))},$$

and hence, the conversion rate in (12.3) can be expressed as

$$\frac{r(t)}{r(t - \tau(t))}b(t - \tau(t))e^{-\int_{t-\tau(t)}^t \mu_1(\xi) d\xi}.$$

Thanks to this relation, we can always assume that $1 - \tau'(t) > 0$ for any biologically reasonable developmental delay.

Next, we extend the two-stage model (12.2) to describe host-parasite interaction, where the parasite developmental duration is dependent on time. Motivated by the fundamental modelling frameworks in Anderson and May [15] and Dobson and Hudson [100], we consider four stages: Free living larvae not infective $X(t)$, free living larvae infective $L(t)$, arrested larvae in the host $Y(t)$, and adult parasites $P(t)$. We are concerned with two delays in the parasite life cycle, one in the free-living stage and the other within the host population: (i) the developmental delay $\tau_L(t)$ between the moment when newly shed parasites enter the environment and the moment they reach the infective larval stage and (ii) the time period $\tau_P(t)$ needed for the arrested larvae infecting the host to develop to pathogenic adults [100]. Since the development time to the infectivity stage depends on metabolic rate and hence the temperature condition, we assume the developmental duration is a time-periodic parameter with the period being one year (365 days) as temperature changes seasonally [250]. Much attention should be paid to estimate these time-dependent delays. Other life cycle components may also be temperature-dependent, and therefore, be periodic in time t .

Host population dynamics may be regulated by parasites, which is a crucial assumption for some host-parasite models [291]. However, here we are more concerned with the reproduction ratio analysis, and therefore, we ignore the host survival or fecundity affected by the arrested parasites since the metabolic activity in arrested larvae is very low [100]. This assumption becomes much more reasonable for farmed animal hosts, whose density is largely controlled by the farm owner [291]. Therefore, the host population $H(t)$ is considered to be seasonal, analogous to those constant host population assumptions in [292, 293, 346].

Based on the conversion rate with periodic delays (12.3), we can write the model system as follows:

$$\begin{aligned} \frac{dX(t)}{dt} &= \lambda P(t) - \mu_X(t)X(t) \\ &\quad - \lambda(1 - \tau'_L(t))P(t - \tau_L(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi) d\xi}, \end{aligned} \quad (12.5a)$$

$$\begin{aligned} \frac{dL(t)}{dt} &= \lambda(1 - \tau'_L(t))P(t - \tau_L(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi) d\xi} - \mu_L(t)L(t) \\ &\quad - \beta(t)H(t)L(t), \end{aligned} \quad (12.5b)$$

$$\begin{aligned} \frac{dY(t)}{dt} &= \beta(t)H(t)L(t) - (\mu_Y(t) + \mu_H(t))Y(t) \\ &\quad - (1 - \tau'_P(t))\beta(t - \tau_P(t))H(t - \tau_P(t)) \times \\ &\quad e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi) + \mu_H(\xi)) d\xi} L(t - \tau_P(t)), \end{aligned} \quad (12.5c)$$

$$\begin{aligned} \frac{dP(t)}{dt} &= (1 - \tau'_P(t))\beta(t - \tau_P(t))H(t - \tau_P(t)) \times \\ &\quad e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi) + \mu_H(\xi)) d\xi} L(t - \tau_P(t)) \\ &\quad - (\mu_P(t) + \mu_H(t))P(t) - \alpha_H \left(1 + \frac{P(t)}{H(t)} \frac{k+1}{k}\right) P(t). \end{aligned} \quad (12.5d)$$

System (12.5) describes the change of densities for the four compartments: (1) The free living larvae $X(t)$ are regained through the birth of adult parasite at rate λ , lost by either mortality (at rate $\mu_X(t)$) or development to free living infected larvae (the last term of equation (12.5a)); (2) The density of free living infected larvae $L(t)$ increases from the development of uninfected larvae (the first term of equation (12.5b)) and decreases with the death rate $\mu_L(t)$ and host uptake at rate $\beta(t)H(t)$, which is dependent on the host population $H(t)$; (3) Ingested larvae $Y(t)$ enter the host population with rate $\beta(t)H(t)$. They stay in the host for $\tau_P(t)$ unit time, which is the developmental duration from infective larvae to adult parasite. The development rate to adult parasite is described by the last term of equation (12.5c). Their density decreases due to the natural death rate $\mu_Y(t)$ and host death rate $\mu_H(t)$ as the larvae will also die when hosts die; (4) The density of adult parasites $P(t)$ increases with the development from larvae (first term of (12.5d)), decreases with the mortality, both the natural death at rate $\mu_P(t)$ and host death at rate $\mu_H(t)$. The burden of adult parasite also decreases due to the aggregated distribution of parasites in the host population, by assuming the distribution of parasites within the host population to be negative binomial with exponent k (also known as aggregation parameter) [15]. As argued previously, we can replace $(1 - \tau'_L(t))$ and $(1 - \tau'_P(t))$, respectively, with the developmental proportions

$$1 - \tau'_L(t) = \frac{r_L(t)}{r_L(t - \tau_L(t))} \text{ and } 1 - \tau'_P(t) = \frac{r_P(t)}{r_P(t - \tau_P(t))},$$

where $r_L(t)$ and $r_P(t)$ are the corresponding developmental proportions.

12.2 Threshold Dynamics

In this section, we first introduce the basic reproduction ratio R_0 for model (12.5), and then establish a threshold-type result on its global dynamics.

In system (12.5), the equations (12.5a) and (12.5c) can be decoupled since variables X and Y do not appear in the other two equations. Therefore, we start with the decoupled system:

$$\begin{aligned} \frac{dL}{dt} &= \lambda(1 - \tau'_L(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi) d\xi} P(t - \tau_L(t)) - \mu_L(t)L(t) - \beta(t)H(t)L(t), \\ \frac{dP}{dt} &= (1 - \tau'_P(t))\beta(t - \tau_P(t))H(t - \tau_P(t))e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi) + \mu_H(\xi)) d\xi} L(t - \tau_P(t)) \\ &\quad - (\mu_P(t) + \mu_H(t))P(t) - \alpha_H \left(1 + \frac{P(t)}{H(t)} \frac{k+1}{k}\right) P(t). \end{aligned} \tag{12.6}$$

Further, we can rewrite the other two variables into integral forms:

$$\begin{aligned} X(t) &= \int_{t-\tau_L(t)}^t \lambda P(\xi) e^{-\int_{\xi}^t \mu_X(s) ds} d\xi, \\ Y(t) &= \int_{t-\tau_P(t)}^t \beta(\xi) H(\xi) L(\xi) e^{-\int_{\xi}^t (\mu_Y(s) + \mu_H(s)) ds} d\xi. \end{aligned} \tag{12.7}$$

Once the dynamics of two variables $L(t)$ and $P(t)$ are obtained, that of $X(t)$ and $Y(t)$ can be deduced naturally.

To address the well-posedness of system (12.6), we introduce some notations. Let $\hat{\tau} = \max\{\max_{t \in [0, \omega]} \tau_L(t), \max_{t \in [0, \omega]} \tau_P(t)\}$ and $\mathcal{X} := C([- \hat{\tau}, 0], \mathbb{R}^2)$ equipped with the maximum norm. For a function $x(\cdot) \in C([- \hat{\tau}, \infty), \mathbb{R}^2)$, we can define $x_t \in \mathcal{X}$ as $x_t(\theta) = x(t + \theta), \forall \theta \in [- \hat{\tau}, 0]$. For any $\phi \in \mathcal{X}$, we define $f(t, \phi) = (f_1(t, \phi), f_2(t, \phi))$ with

$$\begin{aligned} f_1(t, \phi) &= \lambda(1 - \tau'_L(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi) d\xi} \phi_2(-\tau_L(t)) - \mu_L(t)\phi_1(0) - \beta(t)H(t)\phi_1(0), \\ f_2(t, \phi) &= (1 - \tau'_P(t))\beta(t - \tau_P(t))H(t - \tau_P(t))e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi) + \mu_H(\xi)) d\xi} \phi_1(-\tau_P(t)) \\ &\quad - (\mu_P(t) + \mu_H(t) + \alpha_H)\phi_2(0) - \frac{k+1}{k} \frac{\alpha_H}{H(t)} \phi_2^2(0). \end{aligned}$$

Due to the ω -periodicity of $\tau_L(t), \mu_L(t), \beta(t), H(t), \tau_P(t), \mu_P(t)$, and $\mu_H(t)$, it is easy to see that $f(t + \omega, \phi) = f(t, \phi)$. Thus, (12.6) is an ω -periodic functional differential system. For notational simplicity, we rewrite system (12.6) into

$$\begin{aligned} \frac{dL}{dt} &= b_L(t)P(t - \tau_L(t)) - d_L(t)L(t), \\ \frac{dP}{dt} &= b_P(t)L(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t), \end{aligned} \tag{12.8}$$

where

$$\begin{aligned} b_L(t) &= \lambda(1 - \tau'_L(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi) d\xi}, \quad d_L(t) = \mu_L(t) + \beta(t)H(t), \\ b_P(t) &= (1 - \tau'_P(t))\beta(t - \tau_P(t))H(t - \tau_P(t))e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi) + \mu_H(\xi)) d\xi}, \\ d_P(t) &= \mu_P(t) + \mu_H(t) + \alpha_H, \quad \text{and} \quad \alpha(t) = \frac{\alpha_H(k + 1)}{kH(t)}. \end{aligned}$$

Clearly, all these coefficients are positive ω -periodic functions.

For a given continuous ω -periodic function $g(t)$, let

$$\hat{g} = \max_{t \in [0, \omega]} g(t), \quad \bar{g} = \min_{t \in [0, \omega]} g(t).$$

The following result shows that system (12.6) is well-posed on

$$\mathcal{X}_+ := C([- \hat{\tau}, 0], \mathbb{R}_+^2),$$

and hence, the derived model system is also biologically reasonable.

Lemma 12.2.1. *For any $\phi = (\phi_1, \phi_2) \in \mathcal{X}_+$, system (12.6) has a unique nonnegative and bounded solution $v(t, \phi)$ with $v_0 = \phi$ on $[0, \infty)$.*

Proof. Note that $f(t, \phi)$ is continuous and Lipschitzian in ϕ in each compact subset of \mathcal{X}_+ . It follows that for any $\phi \in \mathcal{X}_+$, system (12.6) admits a unique

solution $u(t, \phi)$ with $u_0 = \phi$ on its maximal interval of existence. Let $x^* = (x_1^*, x_2^*) := \left(\frac{\hat{b}_L}{d_L} \frac{\hat{b}_P \hat{b}_L}{\alpha d_L}, \frac{\hat{b}_P \hat{b}_L}{\alpha d_L} \right)$. For any given $\rho \geq 1$, let $[0, \rho x^*]_{\mathcal{X}}$ be the order interval in \mathcal{X} , that is,

$$[0, \rho x^*]_{\mathcal{X}} := \{ \phi \in \mathcal{X} : 0 \leq \phi(\theta) \leq \rho x^*, \forall \theta \in [-\hat{\tau}, 0] \}.$$

It is easy to verify that whenever $\psi \in [0, \rho x^*]_{\mathcal{X}}$, $t \in \mathbb{R}$, and $\psi_i(0) = 0$ ($\psi_i(0) = \rho x_i^*$) for some i , then $f_i(t, \psi) \geq 0$ ($f_i(t, \psi) \leq 0$). By [326, Theorem 5.2.1 and Remark 5.2.1], it follows that $[0, \rho x^*]_{\mathcal{X}}$ is positively invariant for system (12.6). Since ρ can be chosen as large as we wish, this proves the positivity and boundedness of solutions in \mathcal{X}_+ . ■

Next we use the theory in Section 11.1 to introduce the basic reproduction ratio for our model system with periodic time delays. Linearizing system (12.8) at its parasite-free steady state $(0, 0)$, we obtain the following linear periodic system:

$$\begin{aligned} \frac{dL}{dt} &= b_L(t)P(t - \tau_L(t)) - d_L(t)L(t), \\ \frac{dP}{dt} &= b_P(t)L(t - \tau_P(t)) - d_P(t)P(t). \end{aligned} \tag{12.9}$$

Let

$$F(t) \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} b_L(t)\phi_2(-\tau_L(t)) \\ b_P(t)\phi_1(-\tau_P(t)) \end{pmatrix} \text{ and } V(t) = \begin{pmatrix} d_L(t) & 0 \\ 0 & d_P(t) \end{pmatrix}.$$

Then the linear system (12.9) can be written as

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

Note that $F(t)$ and $V(t)$ are ω -periodic in t and the newly “birth” parasites is described by $F(t)$ while the growth of the parasites except birth is described by the following evolution system

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

Let $Z(t, s)$, $t \geq s$, be the evolution matrix of the above linear system. That is, for each $s \in \mathbb{R}$, the 2×2 matrix $Z(t, s)$ satisfies

$$\frac{d}{dt} Z(t, s) = -V(t)Z(t, s), \quad \forall t \geq s, \quad Z(s, s) = I,$$

where I is the 2×2 identity matrix. Clearly, we have

$$Z(t, s) = \begin{pmatrix} e^{-\int_s^t d_L(\xi)d\xi} & 0 \\ 0 & e^{-\int_s^t d_P(\xi)d\xi} \end{pmatrix}.$$

Recall that the exponential growth bound of $Z(t, s)$ is defined as

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

It is easy to see that $\hat{\omega}(Z) \leq -\min\{\bar{d}_L, \bar{d}_P\}$. Therefore, $F(t)$ and $V(t)$ satisfy the following assumptions:

- (A1) $F(t) : \mathcal{X} \rightarrow \mathbb{R}^2$ is positive in the sense that $F(t)\mathcal{X}_+ \subseteq \mathbb{R}_+^2$;
- (A2) The periodic matrix $-V(t)$ is cooperative, and $\hat{\omega}(Z) < 0$.

Let C_ω be the Banach space of all ω -periodic functions from \mathbb{R} to \mathbb{R}^2 , equipped with the maximum norm and the positive cone $C_\omega^+ := \{u \in C_\omega : u(t) \geq 0, \forall t \in \mathbb{R}\}$. Suppose $v \in C_\omega$ is the initial distribution of larval and adult parasites in this periodic environment, then $F(t-s)v_{t-s}$ is the distribution of newly born parasites at time $t-s$ with $t \geq s \geq 0$, and $Z(t, t-s)F(t-s)v_{t-s}$ represents the distribution of those parasites who were newly reproduced at time $t-s$ and still survive in the environment at time t for $t \geq s$. Hence,

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

gives the distribution of accumulative parasite burden at time t produced by those parasites introduced at all previous time.

We define the next generation operator $L : C_\omega \rightarrow C_\omega$ by

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

According to Section 11.1, the basic reproduction ratio is $R_0 := r(L)$, the spectral radius of L .

For any given $t \geq 0$, let $W(t)$ be the time- t map of the linear periodic system (12.9) on \mathcal{X} , that is, $W(t)\phi = w_t(\phi)$, where $w(t, \phi)$ is the unique solution of (12.9) with $w_0 = \phi \in \mathcal{X}$. By Theorem 11.1.1, we have the following result, which indicates that $R_0 - 1$ is a threshold value for the stability of the zero solution of system (12.9).

Lemma 12.2.2. *$R_0 - 1$ has the same sign as $r(W(\omega)) - 1$.*

To study the global dynamics of the model system in terms of R_0 , our strategy is to use the theory of monotone and subhomogeneous semiflows in Section 2.3. We start with a new phase space on which system (12.6) generates an eventually strongly monotone periodic semiflow.

Let

$$\mathcal{Y} := C([-\tau_P(0), 0], \mathbb{R}) \times C([-\tau_L(0), 0], \mathbb{R}),$$

and

$$\mathcal{Y}_+ := C([-\tau_P(0), 0], \mathbb{R}_+) \times C([-\tau_L(0), 0], \mathbb{R}_+).$$

Then $(\mathcal{Y}, \mathcal{Y}_+)$ is an ordered Banach space. For a continuous function $u : [-\tau_P(0), +\infty) \times [-\tau_L(0), +\infty) \rightarrow \mathbb{R}^2$ and $t \geq 0$, we define $u_t \in \mathcal{Y}$ by

$$(u_t)_1(\theta) = u_1(t+\theta), \forall \theta \in [-\tau_P(0), 0], \quad (u_t)_2(\eta) = u_2(t+\eta), \forall \eta \in [-\tau_L(0), 0].$$

Lemma 12.2.3. *For any $\phi \in \mathcal{Y}_+$, system (12.8) admits a unique nonnegative solution $u(t, \phi)$ on $[0, \infty)$ with $u_0 = \phi$.*

Proof. Let $\bar{\tau} = \min\{\bar{\tau}_L, \bar{\tau}_P\}$. For any $t \in [0, \bar{\tau}]$, since $t - \tau_L(t)$ is strictly increasing, we have

$$-\tau_L(0) = 0 - \tau_L(0) \leq t - \tau_L(t) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0,$$

and hence

$$P(t - \tau_L(t)) = \phi_2(t - \tau_L(t)).$$

Similarly,

$$L(t - \tau_P(t)) = \phi_1(t - \tau_P(t)).$$

Therefore, we have the following equations for $t \in [0, \bar{\tau}]$:

$$\begin{aligned} \frac{dL}{dt} &= b_L(t)\phi_2(t - \tau_L(t)) - d_L(t)L(t), \\ \frac{dP}{dt} &= b_P(t)\phi_1(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t). \end{aligned}$$

Given $\phi \in \mathcal{Y}_+$, the solution $(L(t), P(t))$ of the above system exists for $t \in [0, \bar{\tau}]$. In other words, we obtain the values of $u_1(\theta) = L(\theta)$ for $\theta \in [-\tau_P(0), \bar{\tau}]$ and $u_2(\eta) = P(\eta)$ for $\eta \in [-\tau_L(0), \bar{\tau}]$.

For any $t \in [\bar{\tau}, 2\bar{\tau}]$, we have

$$-\tau_L(0) = 0 - \tau_L(0) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq t - \tau_L(t) \leq 2\bar{\tau} - \tau_L(2\bar{\tau}) \leq 2\bar{\tau} - \bar{\tau} = \bar{\tau},$$

and hence, $P(t - \tau_L(t)) = u_2(t - \tau_L(t))$ is known. Similarly, $L(t - \tau_P(t)) = u_1(t - \tau_P(t))$ is also given from the previous step. Solving the following ordinary differential system for $t \in [\bar{\tau}, 2\bar{\tau}]$ with $L(\bar{\tau}) = u_1(\bar{\tau})$ and $P(\bar{\tau}) = u_2(\bar{\tau})$:

$$\begin{aligned} \frac{dL}{dt} &= b_L(t)u_2(t - \tau_L(t)) - d_L(t)L(t), \\ \frac{dP}{dt} &= b_P(t)u_1(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t), \end{aligned}$$

we then get the solution $(L(t), P(t))$ on the interval $[\bar{\tau}, 2\bar{\tau}]$.

We can extend this procedure to $[n\bar{\tau}, (n+1)\bar{\tau}]$ for all $n \in \mathbb{N}$. It then follows that for any initial data $\phi \in \mathcal{Y}_+$, the solution $(L(t), P(t))$ exists uniquely for all $t \geq 0$. ■

Remark 12.2.1. By the uniqueness of solutions in Lemmas 12.2.1 and 12.2.3, it follows that for any $\psi \in \mathcal{X}_+$ and $\phi \in \mathcal{Y}_+$ with $\psi_1(\theta) = \phi_1(\theta), \forall \theta \in [-\tau_P(0), 0]$ and $\psi_2(\eta) = \phi_2(\eta), \forall \eta \in [-\tau_L(0), 0]$, then $u(t, \phi) = v(t, \psi), \forall t \geq 0$, where $u(t, \phi)$ and $v(t, \psi)$ are solutions of system (12.8) satisfying $u_0 = \phi$ and $v_0 = \psi$, respectively.

Lemma 12.2.4. *Let $Q_t(\phi) = u_t(\phi)$, $t \geq 0$. Then Q_t is an ω -periodic semiflow on \mathcal{Y}_+ in the sense that (i) $Q_0 = I$; (ii) $Q_{t+\omega} = Q_t \circ Q_\omega, \forall t \geq 0$; and (iii) $Q_t(\phi)$ is continuous in $(t, \phi) \in [0, \infty) \times \mathcal{Y}_+$.*

Proof. Clearly, property (i) holds true, and property (iii) follows from a standard argument. It suffices to prove (ii). Denote $v(t) = u(t + \omega, \phi)$, we need to show that $v(t) = u(t, u_\omega(\phi)), \forall t \geq 0$. To do this, we first check

$$\begin{aligned} \frac{dv_1(t)}{dt} &= \frac{du_1(t + \omega, \phi)}{dt} \\ &= b_L(t + \omega)u_2(t + \omega - \tau_L(t + \omega), \phi) - d_L(t + \omega)u_1(t + \omega, \phi) \\ &= b_L(t)u_2(t + \omega - \tau_L(t + \omega), \phi) - d_L(t)u_1(t + \omega, \phi) \\ &= b_L(t)v_2(t - \tau_L(t)) - d_L(t)v_1(t). \end{aligned}$$

Similarly, we have

$$\frac{dv_2(t)}{dt} = b_P(t)v_1(t - \tau_P(t)) - d_P(t)v_2(t) - \alpha(t)(v_2(t))^2.$$

This shows that $v(t)$ is also a solution of system (12.8). Moreover, we have $v_1(\theta) = u_1(\theta + \omega, \phi)$ for $\theta \in [-\tau_P(0), 0]$ and $v_2(\eta) = u_2(\eta + \omega, \phi)$ for $\eta \in [-\tau_L(0), 0]$. On the other side, let $w(t) = u(t, u_\omega(\phi))$, then $w(t)$ is also a solution of system (12.8), and $w_1(\theta) = u_1(\theta, u_\omega(\phi)) = u_\omega(\phi)_1(\theta) = u_1(\theta + \omega, \phi)$ for $\theta \in [-\tau_P(0), 0]$ and $w_2(\eta) = u_2(\eta, u_\omega(\phi)) = u_\omega(\phi)_2(\eta) = u_2(\eta + \omega, \phi)$ for $\eta \in [-\tau_L(0), 0]$. Thus, $v(t)$ and $w(t)$ are solutions of system (12.8) with the same initial data. By the uniqueness of solutions, we see that $v(t) = w(t), \forall t \geq 0$, that is,

$$u(t + \omega, \phi) = u(t, u_\omega(\phi)), \quad \forall t \geq 0.$$

For any $t \geq 0$ and $\theta \in [-\tau_P(0), 0]$, if $t + \theta \geq 0$, we have $u_1(t + \theta + \omega, \phi) = u_1(t + \theta, u_\omega(\phi))$, that is, $u_{t+\omega}(\phi)_1(\theta) = u_t \circ u_\omega(\phi)_1(\theta)$; if $t + \theta < 0$, then $u_1(t + \theta, u_\omega(\phi)) = u_\omega(\phi)_1(t + \theta) = u_1(t + \theta + \omega, \phi)$, which also implies $u_t \circ u_\omega(\phi)_1(\theta) = u_{t+\omega}(\phi)_1(\theta)$. Similarly, we can show that $u_t \circ u_\omega(\phi)_2(\eta) = u_{t+\omega}(\phi)_2(\eta)$ for all $\eta \in [-\tau_L(0), 0]$ and $t \geq 0$. It then follows that $u_t \circ u_\omega(\phi) = u_{t+\omega}(\phi)$, and hence, $Q_{t+\omega}(\phi) = Q_t \circ Q_\omega(\phi)$ for all $\phi \in \mathcal{Y}_+$ and $t \geq 0$. ■

The following two lemmas indicate that the periodic semiflow Q_t is eventually strongly monotone and strictly subhomogeneous.

Lemma 12.2.5. *For any ϕ and ψ in \mathcal{Y}_+ with $\phi > \psi$ (that is, $\phi \geq \psi$ but $\phi \neq \psi$), the solutions $u(t)$ and $v(t)$ of system (12.8) with $u_0 = \phi$ and $v_0 = \psi$, respectively, satisfy $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1, 2$, and hence, $Q_t(\phi) \gg Q_t(\psi)$ in \mathcal{Y} for all $t > 3\hat{\tau}$.*

Proof. As in the proof of Lemma 12.2.3, a simple comparison argument on each interval $[n\bar{\tau}, (n + 1)\bar{\tau}]$, $n \in \mathbb{N}$, implies that $u_i(t) \geq v_i(t)$ for all $t \geq 0$. By Lemma 12.2.1 and Remark 12.2.1, both $u(t)$ and $v(t)$ are bounded on $[0, \infty)$, and hence, there exists a real number $b > 0$ such that u_t and v_t are in the

order interval $[(0, 0), (b, b)]_{\mathcal{Y}}$ for all $t \geq 0$. Thus, we can choose a large number $M > 0$ such that for each $t \in \mathbb{R}$, $g_1(t, L) := -d_L(t)L + ML$ is increasing in $L \in [0, b]$ and $g_2(t, P) := -d_P(t)P - \alpha(t)P^2 + MP$ is increasing in $P \in [0, b]$. It then follows that both $u(t)$ and $v(t)$ satisfy the following system of integral equations:

$$\begin{aligned} L(t) &= e^{-Mt}L(0) + \int_0^t e^{-M(t-s)}g_1(s, L(s))ds + \int_0^t e^{-M(t-s)}b_L(s)P(s - \tau_L(s))ds, \\ P(t) &= e^{-Mt}P(0) + \int_0^t e^{-M(t-s)}g_2(s, P(s))ds + \int_0^t e^{-M(t-s)}b_P(s)L(s - \tau_P(s))ds, \end{aligned} \tag{12.10}$$

for all $t \geq 0$. Since both $m_L(t) := t - \tau_L(t)$ and $m_P(t) := t - \tau_P(t)$ are increasing in $t \in \mathbb{R}$, it easily follows that $[-\tau_L(0), 0] \subseteq m_L([0, \hat{\tau}])$ and $[-\tau_P(0), 0] \subseteq m_P([0, \hat{\tau}])$. Without loss of generality, we assume that $\phi_2 > \psi_2$. Then there exists an $\eta \in [-\tau_L(0), 0]$ such that $u_2(\eta) > v_2(\eta)$. In view of the first equation of (12.10), we have $u_1(t) > v_1(t)$ for all $t > \hat{\tau}$. Note that if $s > 2\hat{\tau}$, then $s - \tau_P(s) > 2\hat{\tau} - \hat{\tau} = \hat{\tau}$. By the second equation of (12.10), it follows that $u_2(t) > v_2(t)$ for all $t > 2\hat{\tau}$. This shows that $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1, 2$, and hence, the solution map Q_t is strongly monotone whenever $t > 3\hat{\tau}$. ■

Lemma 12.2.6. *For any $\phi \gg 0$ in \mathcal{Y} and any $\gamma \in (0, 1)$, we have $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$, and hence, $Q_\omega^n(\gamma\phi) \gg \gamma Q_\omega^n(\phi)$ in \mathcal{Y} for all integers n with $n\omega > 2\hat{\tau}$.*

Proof. Let $w(t) = u(t, \gamma\phi)$ and $v(t) = \gamma u(t, \phi)$, where $u(t, \phi)$ is the unique solution of system (12.8) with $u_0 = \phi \gg 0$ in \mathcal{Y} . As in the proof of Lemma 12.2.3, we see that $w(t) > 0$ and $v(t) > 0$ for all $t \geq 0$. Moreover, for all $\theta \in [-\tau_P(0), 0]$ and $\eta \in [-\tau_L(0), 0]$, we have

$$w_1(\theta) = \gamma\phi_1(\theta) = v_1(\theta) \text{ and } w_2(\eta) = \gamma\phi_2(\eta) = v_2(\eta).$$

It is easy to see that $v(t)$ satisfies the following system:

$$\begin{aligned} \frac{dv_1(t)}{dt} &= b_L(t)v_2(t - \tau_L(t)) - d_L(t)v_1(t), \\ \frac{dv_2(t)}{dt} &= b_P(t)v_1(t - \tau_P(t)) - d_P(t)v_2(t) - \frac{\alpha(t)}{\gamma}v_2^2(t), \end{aligned}$$

and hence,

$$v_1(t) = \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right] \exp\left(-\int_0^t d_L(\eta)d\eta\right)$$

for all $t \geq 0$. For any $0 \leq t \leq \bar{\tau}$, we have

$$-\tau_L(0) \leq t - \tau_L(t) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq 0$$

and

$$\begin{aligned} w_1(t) &= \left[w_1(0) + \int_0^t b_L(\xi)w_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right] \exp\left(-\int_0^t d_L(\eta)d\eta\right) \\ &= \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right] \exp\left(-\int_0^t d_L(\eta)d\eta\right) \\ &= v_1(t). \end{aligned}$$

On the other side, the derivative of $v_2(t)$ at $t = 0$:

$$\begin{aligned} \left. \frac{dv_2(t)}{dt} \right|_{t=0} &= b_P(0)v_1(0 - \tau_P(0)) - d_P(0)v_2(0) - \frac{\alpha(0)}{\gamma}v_2^2(0) \\ &< b_P(0)v_1(0 - \tau_P(0)) - d_P(0)v_2(0) - \alpha(0)v_2^2(0) \\ &= b_P(0)w_1(-\tau_P(0)) - d_P(0)w_2(0) - \alpha(0)w_2^2(0) \\ &= \left. \frac{dw_2(t)}{dt} \right|_{t=0}. \end{aligned}$$

Since $v_2(0) = w_2(0) > 0$, it follows that there exists an $\epsilon \in (0, \bar{\tau})$ such that $0 < v_2(t) < w_2(t)$ for all $0 < t < \epsilon$. We claim that $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$. Assume not, then there exists $t_0 \in (0, \bar{\tau}]$ such that $v_2(t) < w_2(t)$ for all $0 < t < t_0$ while $v_2(t_0) = w_2(t_0)$, which implies $v_2'(t_0) \geq w_2'(t_0)$. However, we have

$$\begin{aligned} \left. \frac{dv_2(t)}{dt} \right|_{t=t_0} &= b_P(t_0)v_1(t_0 - \tau_P(t_0)) - d_P(t_0)v_2(t_0) - \frac{\alpha(t_0)}{\gamma}v_2^2(t_0) \\ &< b_P(t_0)v_1(t_0 - \tau_P(t_0)) - d_P(t_0)v_2(t_0) - \alpha(t_0)v_2^2(t_0) \\ &= b_P(t_0)w_1(t_0 - \tau_P(t_0)) - d_P(t_0)w_2(t_0) - \alpha(t_0)w_2^2(t_0) \\ &= \left. \frac{dw_2(t)}{dt} \right|_{t=t_0}, \end{aligned}$$

a contradiction. This shows that $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$.

Similar arguments for any interval $(n\bar{\tau}, (n+1)\bar{\tau}]$ imply that $v_1(t) \leq w_1(t)$ and $v_2(t) < w_2(t)$ for all $t \in (n\bar{\tau}, (n+1)\bar{\tau}]$ with $n \in \mathbb{N}$. In particular, $\xi - \tau_L(\xi) > \hat{\tau} - \hat{\tau} = 0$ and $w_2(\xi - \tau_L(\xi)) > v_2(\xi - \tau_L(\xi))$ for all $\xi > \hat{\tau}$. Therefore, for any $t > \hat{\tau}$, we have

$$\begin{aligned} w_1(t) &= \left[w_1(0) + \int_0^t b_L(\xi)w_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right] \exp\left(-\int_0^t d_L(\eta)d\eta\right) \\ &> \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi - \tau_L(\xi)) \exp\left(\int_0^\xi d_L(\eta)d\eta\right)d\xi \right] \exp\left(-\int_0^t d_L(\eta)d\eta\right) \\ &= v_1(t). \end{aligned}$$

It follows that $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$ for all $t > \hat{\tau}$, that is, $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$. Thus, $Q_\omega^n(\gamma\phi) = Q_{n\omega}(\gamma\phi) \gg \gamma Q_{n\omega}(\phi) = \gamma Q_\omega^n(\phi)$ for all integer n with $n\omega > 2\hat{\tau}$. ■

For any given $t \geq 0$, let $G(t)$ be the time- t map of the linear periodic system (12.9) on \mathcal{Y} , that is, $G(t)\phi = z_t(\phi)$, where $z(t, \phi)$ is the unique solution of (12.9) with $z_0 = \phi \in \mathcal{Y}$. The subsequent result shows that the stability of the zero solution for system (12.9) on \mathcal{X} is equivalent to that on \mathcal{Y} .

Lemma 12.2.7. *Two Poincaré maps $W(\omega) : \mathcal{X} \rightarrow \mathcal{X}$ and $G(\omega) : \mathcal{Y} \rightarrow \mathcal{Y}$ have the same spectral radius, that is, $r(W(\omega)) = r(G(\omega))$.*

Proof. We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. By the proof of Lemma 12.2.5, we see that $G(\omega)^{n_0} = G(n_0\omega)$ is strongly positive on \mathcal{Y} . Further, [145, Theorem 3.6.1] implies that $G(\omega)^{n_0}$ is compact. Then $r(G(\omega)) > 0$ according to the Krein-Rutmann theorem, as applied to the linear operator $(G(\omega))^{n_0}$, together with the fact that $r_n(G(\omega)^{n_0}) = (r(G(\omega)))^{n_0}$. For any given $\phi = (\phi_1, \phi_2) \in \mathcal{Y}$, we define $\tilde{\phi} = (\tilde{\phi}_1, \tilde{\phi}_2) \in \mathcal{X}$ by

$$\tilde{\phi}_1(\theta) = \begin{cases} \phi_1(-\tau_P(0)) & \text{if } \theta \in [-\hat{\tau}, -\tau_P(0)], \\ \phi_1(\theta) & \text{if } \theta \in [-\tau_P(0), 0]; \end{cases}$$

and

$$\tilde{\phi}_2(\theta) = \begin{cases} \phi_2(-\tau_L(0)) & \text{if } \theta \in [-\hat{\tau}, -\tau_L(0)], \\ \phi_2(\theta) & \text{if } \theta \in [-\tau_L(0), 0]. \end{cases}$$

Clearly, $\|\phi\|_{\mathcal{Y}} = \|\tilde{\phi}\|_{\mathcal{X}}$. By Remark 12.2.1, it follows that for all integer n with $n\omega > \hat{\tau}$,

$$\|G(n\omega)\phi\|_{\mathcal{Y}} \leq \|W(n\omega)\tilde{\phi}\|_{\mathcal{X}} \leq \|W(n\omega)\|_{\mathcal{X}} \cdot \|\tilde{\phi}\|_{\mathcal{X}} = \|W(n\omega)\|_{\mathcal{X}} \cdot \|\phi\|_{\mathcal{Y}}, \quad \forall \phi \in \mathcal{Y},$$

and hence, $\|G(n\omega)\|_{\mathcal{Y}} \leq \|W(n\omega)\|_{\mathcal{X}}$. Since

$$r(G(\omega)) = \lim_{n \rightarrow \infty} \|G(\omega)^n\|_{\mathcal{Y}}^{\frac{1}{n}} = \lim_{n \rightarrow \infty} \|G(n\omega)\|_{\mathcal{Y}}^{\frac{1}{n}}$$

and

$$r(W(\omega)) = \lim_{n \rightarrow \infty} \|W(\omega)^n\|_{\mathcal{X}}^{\frac{1}{n}} = \lim_{n \rightarrow \infty} \|W(n\omega)\|_{\mathcal{X}}^{\frac{1}{n}},$$

we then have $r(W(\omega)) \geq r(G(\omega)) > 0$.

It remains to prove that $r(W(\omega)) \leq r(G(\omega))$. In view of [326, Theorem 5.1.1] and [145, Theorem 3.6.1], we see that the linear operator $W(\omega)^{n_0} = W(n_0\omega)$ is positive and compact on \mathcal{X} . By the Krein-Rutmann theorem (see, e.g., [152, Theorem 7.1]), $r(W(\omega)^{n_0})$ is an eigenvalue of $W(\omega)^{n_0}$ with an eigenvector $\phi^* > 0$ in \mathcal{X} . For any $\phi \in \mathcal{X}$, we define $\underline{\phi} \in \mathcal{Y}$ as

$$\underline{\phi}_1(\theta) = \phi_1(\theta), \quad \forall \theta \in [-\tau_P(0), 0], \quad \text{and} \quad \underline{\phi}_2(\eta) = \phi_2(\eta), \quad \forall \eta \in [-\tau_L(0), 0].$$

By Remark 12.2.1, we have $u(t, \phi) = v(t, \underline{\phi})$, $\forall t \geq 0$, where $u(t, \phi)$ and $v(t, \underline{\phi})$ are the unique solutions of system (12.9) with $u_0 = \phi \in \mathcal{X}$ and $v_0 = \underline{\phi} \in \mathcal{Y}$, respectively. We further claim that $\underline{\phi}^* > 0$ in \mathcal{Y} . Otherwise, $\underline{\phi}^* = \underline{0}$, and

hence, $u(t, \phi^*) = v(t, \phi^*) = 0, \forall t \geq 0$. This implies that

$$(r(W(\omega)))^{n_0} \phi^* = r(W(\omega)^{n_0}) \phi^* = W(\omega)^{n_0} \phi^* = W(n_0\omega) \phi^* = 0,$$

and hence, $\phi^* = 0$ in \mathcal{X} , which is a contradiction. Since

$$G(\omega)^{n_0} \phi^* = \underline{W(\omega)^{n_0} \phi^*} = \underline{r(W(\omega)^{n_0}) \phi^*} = (r(W(\omega)))^{n_0} \phi^*,$$

$(r(W(\omega)))^{n_0}$ is a positive eigenvalue of $G(\omega)^{n_0}$ with ϕ^* being a positive eigenvector in \mathcal{Y} . It then follows that $(r(W(\omega)))^{n_0} \leq r(G(\omega)^{n_0}) = (r(G(\omega)))^{n_0}$, and hence $r(W(\omega)) \leq r(G(\omega))$. Consequently, we have $r(W(\omega)) = r(G(\omega))$. ■

Now we are in a position to prove the main result of this section.

Theorem 12.2.1. *The following statements are valid:*

- (1) *If $R_0 \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (12.8) in \mathcal{Y}_+ .*
- (2) *If $R_0 > 1$, then system (12.8) admits a unique positive ω -periodic solution $(L^*(t), P^*(t))$, and it is globally asymptotically stable for system (12.8) in $\mathcal{Y}_+ \setminus \{(0, 0)\}$.*

Proof. We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. In view of Lemma 12.2.4, Q_t can be regarded as an $n_0\omega$ -periodic semiflow on \mathcal{Y}_+ . By Lemmas 12.2.5 and 12.2.6, $Q_{n_0\omega}$ is a strongly monotone and strictly subhomogeneous map on \mathcal{Y}_+ . Applying Theorem 2.3.4 and Lemma 2.2.1 to the map $Q_{n_0\omega}$, we have the following threshold-type result:

- (a) *If $r(DQ_{n_0\omega}(0)) \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (12.8) in \mathcal{Y}_+ .*
- (b) *If $r(DQ_{n_0\omega}(0)) > 1$, then system (12.8) admits a unique positive $n_0\omega$ -periodic solution $(L^*(t), P^*(t))$, and it is globally asymptotically stable for system (12.8) in $\mathcal{Y}_+ \setminus \{(0, 0)\}$.*

Note that $r(DQ_{n_0\omega}(0)) = r(G(n_0\omega)) = (r(G(\omega)))^{n_0}$. By Lemmas 12.2.2 and 12.2.7, we then see that

$$\text{sign}(R_0 - 1) = \text{sign}(r(DQ_{n_0\omega}(0)) - 1).$$

Thus, it suffices to show that in case (b), $(L^*(t), P^*(t))$ is also ω -periodic. Let $\psi^* = v_0^* \in \mathcal{Y}$ with $v^*(t) = (L^*(t), P^*(t))$. Then $Q_{n_0\omega} \psi^* = \psi^*$. Note that

$$Q_\omega^{n_0}(Q_\omega \psi^*) = Q_\omega(Q_\omega^{n_0} \psi^*) = Q_\omega(Q_{n_0\omega} \psi^*) = Q_\omega(\psi^*).$$

By the uniqueness of the positive fixed point of $Q_\omega^{n_0} = Q_{n_0\omega}$, it follows that $Q_\omega \psi^* = \psi^*$, which implies that $(L^*(t), P^*(t)) = u(t, \psi^*)$ is an ω -periodic solution of system (12.8). ■

In the rest of this section, we deduce the dynamics for the other two variables $X(t)$ and $Y(t)$ in system (12.5), which do not appear in system (12.6). In the case where $R_0 > 1$, we have

$$\lim_{t \rightarrow \infty} [(L(t), P(t)) - (L^*(t), P^*(t))] = 0$$

for any solution of system (12.6) through nonzero initial data. By using the integral form for the free living uninfected larvae $X(t)$ and arrested larvae $Y(t)$ in (12.7), we obtain

$$\begin{aligned} \lim_{t \rightarrow \infty} \left[X(t) - \int_{t-\tau_L}^t \lambda P^*(\xi) e^{-\int_{\xi}^t \mu_X(s) ds} d\xi \right] &= 0, \text{ and} \\ \lim_{t \rightarrow \infty} \left[Y(t) - \int_{t-\tau_P}^t \beta(\xi) H(\xi) L^*(\xi) e^{-\int_{\xi}^t (\mu_Y(s) + \mu_H(s)) ds} d\xi \right] &= 0. \end{aligned}$$

Moreover, it is easy to verify that both

$$X^*(t) := \int_{t-\tau_L}^t \lambda P^*(\xi) e^{-\int_{\xi}^t \mu_X(s) ds} d\xi$$

and

$$Y^*(t) := \int_{t-\tau_P}^t \beta(\xi) H(\xi) L^*(\xi) e^{-\int_{\xi}^t (\mu_Y(s) + \mu_H(s)) ds} d\xi$$

are positive ω -periodic functions. In the case where $R_0 \leq 1$, we have

$$\lim_{t \rightarrow \infty} (L(t), P(t)) = (0, 0).$$

By using the integral form in (12.7) again, we obtain

$$\lim_{t \rightarrow \infty} (X(t), Y(t)) = (0, 0).$$

In summary, we have the following result on the global dynamics of the full model system.

Theorem 12.2.2. *The following statements hold for system (12.5):*

- (1) *If $R_0 \leq 1$, then $(0, 0, 0, 0)$ is globally attractive.*
- (2) *If $R_0 > 1$, then there exists a positive ω -periodic solution*

$$(X^*(t), L^*(t), Y^*(t), P^*(t)),$$

and it is globally attractive for all nontrivial solutions.

12.3 Numerical Computation of R_0

To numerically compute the basic reproduction ratio, we are going to rewrite the linear operator L into the form of equation (3) in [282], where an algorithm is proposed for the R_0 computation of periodic ordinary differential systems.

Note that

$$F(t-s) \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} b_L(t-s)\phi_2(-\tau_L(t-s)) \\ b_P(t-s)\phi_1(-\tau_P(t-s)) \end{pmatrix}.$$

It then follows that

$$\begin{aligned} [Lv](t) &= \int_0^\infty Z(t, t-s)F(t-s)v(t-s+\cdot)ds \\ &= \int_0^\infty \begin{pmatrix} e^{-\int_{t-s}^t d_L(\xi)d\xi} & 0 \\ 0 & e^{-\int_{t-s}^t d_P(\xi)d\xi} \end{pmatrix} \begin{pmatrix} b_L(t-s)v_2(t-s-\tau_L(t-s)) \\ b_P(t-s)v_1(t-s-\tau_P(t-s)) \end{pmatrix} ds \\ &= \begin{pmatrix} \int_0^\infty e^{-\int_{t-s}^t d_L(\xi)d\xi} b_L(t-s)v_2(t-s-\tau_L(t-s))ds \\ \int_0^\infty e^{-\int_{t-s}^t d_P(\xi)d\xi} b_P(t-s)v_1(t-s-\tau_P(t-s))ds \end{pmatrix}. \end{aligned}$$

Let $t-s-\tau_L(t-s) = t-s_1$. Since the function $y = x - \tau_L(x)$ is strictly increasing, the inverse function exists and we can solve $x = h_L(y)$. Hence, we obtain $t-s = h_L(t-s_1)$, that is,

$$s = t - h_L(t-s_1), \quad ds_1 = d(s + \tau_L(t-s)) = (1 - \tau'_L(t-s))ds,$$

and $ds = \frac{1}{1-\tau'_L(h_L(t-s_1))} ds_1$. Therefore,

$$\begin{aligned} &\int_0^\infty e^{-\int_{t-s}^t d_L(\xi)d\xi} b_L(t-s)v_2(t-s-\tau_L(t-s))ds \\ &= \int_{\tau_L(t)}^\infty \frac{e^{-\int_{h_L(t-s_1)}^t d_L(\xi)d\xi} b_L(h_L(t-s_1))v_2(t-s_1)}{1-\tau'_L(h_L(t-s_1))} ds_1 \\ &= \int_{\tau_L(t)}^\infty \frac{e^{-\int_{h_L(t-s)}^t d_L(\xi)d\xi} b_L(h_L(t-s))v_2(t-s)}{1-\tau'_L(h_L(t-s))} ds. \end{aligned}$$

Similarly, let $t-s-\tau_P(t-s) = t-s_2$. Assume that the inverse function of $y = x - \tau_P(x)$ is $y = h_P(x)$. Solving $t-s = h_P(t-s_2)$, we get

$$s = t - h_P(t-s_2), \quad ds_2 = (1 - \tau'_P(t-s))ds, \quad \text{and} \quad ds = \frac{1}{1 - \tau'_P(h_P(t-s_2))} ds_2.$$

Therefore,

$$\begin{aligned} &\int_0^\infty e^{-\int_{t-s}^t d_P(\xi)d\xi} b_P(t-s)v_1(t-s-\tau_P(t-s))ds \\ &= \int_{\tau_P(t)}^\infty \frac{e^{-\int_{h_P(t-s_2)}^t d_P(\xi)d\xi} b_P(h_P(t-s_2))v_1(t-s_2)}{1-\tau'_P(h_P(t-s_2))} ds_2 \\ &= \int_{\tau_P(t)}^\infty \frac{e^{-\int_{h_P(t-s)}^t d_P(\xi)d\xi} b_P(h_P(t-s))v_1(t-s)}{1-\tau'_P(h_P(t-s))} ds. \end{aligned}$$

Define

$$K_{12}(t, s) = \begin{cases} 0, & s < \tau_L(t) \\ \frac{e^{-\int_{h_L(t-s)}^t d_L(\xi) d\xi} b_L(h_L(t-s))}{1-\tau'_L(h_L(t-s))}, & s \geq \tau_L(t) \end{cases}$$

and

$$K_{21}(t, s) = \begin{cases} 0, & s < \tau_P(t) \\ \frac{e^{-\int_{h_P(t-s)}^t d_P(\xi) d\xi} b_P(h_P(t-s))}{1-\tau'_P(h_P(t-s))}, & s \geq \tau_P(t) \end{cases}$$

while $K_{11}(t, s) = K_{22}(t, s) = 0$. Then we have

$$\begin{aligned} [Lv](t) &= \int_0^\infty K(t, s)v(t-s)ds \\ &= \sum_{j=0}^\infty \int_{j\omega}^{(j+1)\omega} K(t, s)v(t-s)ds \\ &= \sum_{j=0}^\infty \int_0^\omega K(t, j\omega + s)v(t-s-j\omega)ds \\ &= \int_0^\omega G(t, s)v(t-s)ds \end{aligned}$$

with

$$G(t, s) = \sum_{j=0}^\infty K(t, j\omega + s),$$

which is of the integral form

$$[L\phi](t) = \int_0^\omega G(t, s)\phi(t-s)ds. \tag{12.11}$$

Below we present a numerical algorithm, which is due to Posny and Wang [282], for the computation of the spectral radius of the integral operator given by (12.11).

Let us partition the interval $[0, \omega]$ uniformly into n nodes labeled as $t_i = i \cdot \frac{\omega}{n}$ for $i = 0, \dots, n-1$. Using the trapezoidal rule, one of the most common numerical integration techniques, we can approximate the integral in (12.11) with second-order accuracy:

$$[L\phi](t) \approx \frac{\omega}{n} \left(\sum_{i=1}^{n-1} G(t, t_i)\phi(t-t_i) + \frac{1}{2}G(t, t_0)\phi(t-t_0) + \frac{1}{2}G(t, t_n)\phi(t-t_n) \right).$$

Since $\phi(t)$ is ω -periodic, it is clear that $\phi(t-t_0) = \phi(t-t_n)$. For convenience, we let

$$\tilde{G}(t, t_0) = \frac{1}{2}[G(t, t_0) + G(t, t_n)].$$

Then

$$[L\phi](t) \approx \frac{\omega}{n} \left[\tilde{G}(t, t_0)\phi(t-t_0) + \sum_{i=1}^{n-1} G(t, t_i)\phi(t-t_i) \right].$$

Now $[L\phi](t) = \lambda\phi(t)$ can be written as a matrix equation:

$$\frac{\omega}{n} [\tilde{G}(t, t_0) \ G(t, t_1) \ G(t, t_2) \ \cdots \ G(t, t_{n-1})] \begin{bmatrix} \phi(t - t_0) \\ \phi(t - t_1) \\ \phi(t - t_2) \\ \vdots \\ \phi(t - t_{n-1}) \end{bmatrix} = \lambda \phi(t).$$

Setting $t = t_j (0 \leq j \leq n - 1)$ in the above equation yields

$$\frac{\omega}{n} [\tilde{G}(t_j, t_0) \ G(t_j, t_1) \ G(t_j, t_2) \ \cdots \ G(t_j, t_{n-1})] \begin{bmatrix} \phi(t_j - t_0) \\ \phi(t_j - t_1) \\ \phi(t_j - t_2) \\ \vdots \\ \phi(t_j - t_{n-1}) \end{bmatrix} = \lambda \phi(t_j). \quad (12.12)$$

Again, by the periodicity of $\phi(t)$, it follows that

$$\begin{aligned} \phi(t_j - t_0) &= \phi(t_j), & \phi(t_j - t_1) &= \phi(t_{j-1}), & \dots, \\ \phi(t_j - t_{j-1}) &= \phi(t_1), & \phi(t_j - t_j) &= \phi(t_0), & \phi(t_j - t_{j+1}) &= \phi(t_{n-1}), \\ \dots, & & \phi(t_j - t_{n-2}) &= \phi(t_{j+2}), & \phi(t_j - t_{n-1}) &= \phi(t_{j+1}), \end{aligned}$$

and we can rearrange the terms in (12.12) to obtain

$$\frac{\omega}{n} \left[G(t_j, t_j) \ \dots \ \tilde{G}(t_j, t_0) \ G(t_j, t_{n-1}) \ \dots \ G(t_j, t_{j+1}) \right] \begin{bmatrix} \phi(t_0) \\ \phi(t_1) \\ \vdots \\ \phi(t_j) \\ \vdots \\ \phi(t_{n-2}) \\ \phi(t_{n-1}) \end{bmatrix} = \lambda \phi(t_j). \quad (12.13)$$

Note that this equation holds for all $j = 0, \dots, n - 1$, and hence, it generates a matrix system. The coefficient matrix, denoted by A , is given by

$$A = \begin{bmatrix} \tilde{G}(t_0, t_0) & G(t_0, t_{n-1}) & \cdots & \cdots & \cdots & G(t_0, t_2) & G(t_0, t_1) \\ G(t_1, t_1) & \tilde{G}(t_1, t_0) & \cdots & \cdots & \cdots & G(t_1, t_3) & G(t_1, t_2) \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots & \vdots \\ G(t_j, t_j) & G(t_j, t_{j-1}) & \cdot & \tilde{G}(t_j, t_0) & \cdot & G(t_j, t_{j+2}) & G(t_j, t_{j+1}) \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots & \vdots \\ G(t_{n-2}, t_{n-2}) & G(t_{n-2}, t_{n-3}) & \dots & \cdots & \cdots & \tilde{G}(t_{n-2}, t_0) & G(t_{n-2}, t_{n-1}) \\ G(t_{n-1}, t_{n-1}) & G(t_{n-1}, t_{n-2}) & \cdots & \cdots & \cdots & G(t_{n-1}, t_1) & \tilde{G}(t_{n-1}, t_0) \end{bmatrix}. \quad (12.14)$$

It then follows that (12.13) can be put into a compact form:

$$\frac{\omega}{n} A \tilde{\phi} = \lambda \tilde{\phi}, \quad (12.15)$$

where A , defined in (12.14), is a matrix of dimension $(nm) \times (nm)$, and $\tilde{\phi} = [\phi(t_0), \phi(t_1), \dots, \phi(t_{n-1})]^T$ is a vector of dimension $(nm) \times 1$.

Consequently, to compute the basic reproduction ratio $R_0 := \rho(L)$, it suffices to find the maximum λ such that (12.15) is valid, that is, $R_0 \approx \frac{\omega}{n} \rho(A)$.

12.4 Notes

Sections 12.1, 12.2, and 12.3 are taken from Lou and Zhao [234] with the exception that the numerical algorithm in Section 12.3 comes from Posny and Wang [282].

The introduction of the term $1 - \tau'(t)$ is due to the incorporation of state-dependent delay in Barbarossa, Haderer and Kuttler [26] and Kloosterman, Campbell and Poulin [202]. A similar term was formulated in models proposed by Wu et al. [414] and some others, see, e.g., McCauley et al. [246] and the references therein, to describe the population growth with threshold age τ depending on time t .

Model (12.6) was proposed earlier by Molnár et al. [250], where L in equations (8b) and (1b) should be $L(t - \tau_P)$. There are also some other algorithms to compute R_0 for periodic population models with constant time delay, see, e.g., Bacaër [21].