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A periodic delay differential system for mosquito control with *Wolbachia* incompatible insect technique

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Abstract

Wolbachia incompatible insect technique (IIT) depends on releasing male-only *Wolbachia*-infected mosquitoes to reduce/eradicate wild type mosquito populations. Mathematical models can be utilised to help investigate the altered mosquito population dynamics under IIT and propose the appropriate releasing strategies. Incorporating seasonal temperature variations and larval competition, a delayed periodic stage structured model is formulated, which is essentially different from existing models since additional density-dependent death rate due to larval competition introduces a density-dependent survival probability of larvae. This novel feature brings new challenges to mathematical analysis and further model extension in studying the dynamics of mosquito borne diseases (MBDs). By assuming continuous proportional releasing strategies, threshold dynamics in terms of the basic offspring number R_0 are established by employing the dynamical system approach. The mosquito population size is shown to either go extinction if $R_0 < 1$ or stabilize at a periodic pattern when $R_0 > 1$. Then, we numerically explore the seasonal effects on R_0 and the impact of larval competition and released amount of *Wolbachia*-infected males under two levels of mosquito control objectives, i.e., population eradication and reduction. Overestimates of R_0 are observed if seasonality is ignored. The ratio of released *Wolbachia*-infected males to wild type males (the overflooding ratio, p_w) and larval competition are shown to play positive roles in reducing both the required time for population eradication and ultimate adult peak abundance. In particular, the initial population size is negatively correlated with the eradication time, which can be shorten to a minimum of 5 years. In summary, IIT alone may be difficult to eradicate/reduce the mosquito population. Other conventional mosquito control approaches such as spraying larvicides should be used in combination to efficiently control mosquitoes.

Keywords: *Wolbachia* IIT, larval competition, mosquito control, seasonal effects

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1. Introduction

Mosquitoes, especially *Aedes aegypti* and *Aedes albopictus*, are the major vector carrying several arboviruses including dengue, yellow fever, chikungunya and Zika virus, which can be transmitted to humans through biting [1]. These mosquito-borne human diseases pose a

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huge threat to global health. To date, the majority of mosquito borne diseases lack effective targeted treatment or vaccines [2]. As a consequence, suppressing wild *Aedes* mosquito populations becomes the primary strategy to mitigate the transmission. Conventional mosquito control approach is killing mosquitoes by spraying insecticides. However, mosquitoes have developed high resistance to commonly-used insecticides, which reduces the efficiency of this conventional control method. Recent advanced biotechnologies contribute to generating several new environmental friendly vector control approaches, which rely on deploying modified mosquitoes into the field to suppress or replace wild type mosquitoes. Modified mosquitoes can be generated by genetic based techniques [3], irradiated by sterile insect techniques (SIT) [4] or transfected by specific *Wolbachia* strain [5].

Unlike other gene drive approaches, *Wolbachia* based mosquito control approaches do not bring many ethical and regulatory issues [6]. Besides, *Wolbachia*-infected mosquitoes possess lower fitness cost than genetically modified and irradiated (by SIT) mosquitoes [7]. These traits make *Wolbachia* based methods well-accepted and promising alternatives for mosquito control techniques. Owing to maternal transmissibility and cytoplasmic incompatibility (CI) of *Wolbachia*, wild mosquito population can be either suppressed or replaced via releasing mosquitoes transfected by specific *Wolbachia* strain. Due to releasing only non-biting male *Wolbachia* infected mosquitoes, *Wolbachia* incompatible insect technique (IIT) as a population suppression method receives relative higher public acceptance than *Wolbachia* based population replacement approach [8]. Effective population suppression/eradication is caused by reproductive incompatibility of *Wolbachia*-infected males when mating with wild *Wolbachia*-free females [9]. Field male-only releases of *Wolbachia*-infected *Aedes* mosquitoes have been successfully conducted in many countries including Singapore [10], China [11], Australia [12] and United states [13]. Taking China as an example, millions of irradiated triple-*Wolbachia* infected adult males were reared by 'mosquito factory'. In 2016 and 2017, field release trials were conducted by releasing these *Wolbachia* infected males weekly with the yearly averaged overflooding ratios ranging from $8.7 - 15.8$ on the Shazai island, where successful suppression of mosquito population was achieved [14]. Here, the overflooding ratio (OFR) is often employed in *Wolbachia* involved releasing trials to quantify the ratio of released *Wolbachia* infected males to wild-type males [7].

In designing field release trials, mathematical models can be employed to inform proper releasing strategies by evaluating its impact on population dynamics of wild mosquitoes. The modeling mechanism of IIT is analogous to that of SIT, which has been extensively investigated in many studies [15–18]. Modeling studies of IIT can focus on the population dynamics of wild mosquitoes as the dynamics of released sexually active male *Wolbachia* infected mosquitoes is simple and independent [19]. Optimal releasing strategy on suppressing/eradicating the wild mosquito population is the pivotal problem to focus. To investigate practical *Wolbachia* driven mosquito suppression/extinction strategies, a variety of mosquito population models have been developed and analyzed, including discrete dynamical models [20–22], ordinary differential systems [23, 24] and delay differential equation models [25–28].

Two aspects closely related to mosquito growth are often ignored in the majority of modeling studies on mosquito control, especially in mathematical analysis oriented investigations. One is the intraspecific competition during larval stage, which typically occurs in the growth of container-inhabiting *Aedes* mosquitoes [29]. Excluding larval density dependent competition in mathematical modeling may be improper to predict the dynamics of mosquito populations. Density dependent birth and death rates are two common ways incorporating the impacts of larval competition in modeling studies. Studies considering density dependent birth rate usually express it as a natural exponential decaying function of the total population size [30, 31] or as a logistic form with carrying capacity, where the aquatic stages may be included or excluded [32–35]. Other modeling studies explicitly used density dependent death rate in the larval stage [22, 24–26] or in the adult stage [36–39]. Recent experimental studies showed accumulating evidences that juvenile developmental rate and survival of *Ae. aegypti* were significantly affected by the variations of density in larval stage [40, 41]. Hence, it is imperative to seek alternative model forms to incorporate larval competition.

To address this aspect, one can start from an age-structured partial differential equation with a nonlinear term, and reformulate it into delay differential equations (DDEs) describing the population growth within different stages such as immature (larval) and adult stages. These delay equations describe larval competition effects in terms of additional density-dependent death and development rates. The form of the nonlinear term will determine the complexity of the reduced DDE model and further mathematical analysis [42]. For instance, the analysis of the reduced model in Fang et al. [43] becomes challenging when the nonlinearity is modelled as a general nonlinear function of larval population size. Inspired by the modeling idea proposed by Gourley and Liu [44, 45], in the current study, we model the larval competitive effect by a quadratic function of the larval density in the age structured model. The reduced delay equation for adults containing the term quantifying larval intra-specific competition can be decoupled, which makes it mathematically tractable and facilitates further model extension.

The other aspect strongly affecting mosquito population growth is seasonal variations. In particular, seasonal changes of temperature influence almost all activities in the life cycle of mosquitoes including egg laying rate, developmental duration and mortality rates [46, 47]. A number of models incorporating the effects of temperature variations have been developed recently to investigate the mosquito population dynamics [48–51] and control strategies for mosquito borne diseases [52–54]. However, few modeling studies consider the impact of seasonal effects on *Wolbachia* based mosquito control. This further motivates us to quantify the joint effects of larval competition and seasonal environmental variations on mosquito population growth under IIT.

Compared with *Wolbachia* based replacement, long-term sustainable suppression and elimination requires frequently releasing large amount of male *Wolbachia* infected mosquitoes. Fortunately, latest automated processes integrating machine learning can contribute to perfect sex-sorting and efficient amount for continual daily releases, which enable the realization of large-scale suppression [55]. In this paper, we assume a continuous releasing. Under the premise of perfect sex-sorting and continuous releasing, the extent of population suppression/elimination depends crucially on the releasing strategy involving the optimal released amount and initial timing. Rather than constant release strategies, we assume a proportional release strategy where the released amount mosquitoes is adjusted as the product of the overflooding ratio (OFR) and existing wild male population size. One of our essential technical issue is to investigate the integrated impact of the overflooding ratio and larval competition based on a seasonal mosquito stage structured model. The rest of this manuscript is organized as follows. Section 2 provides the detailed derivation of the new stage structured model describing larval competition and seasonal environmental effects, as well as releasing strategies of *Wolbachia* infected males. Section 3 presents dynamical analysis on the model and Section 4 performs numerical simulation to illustrate the effectiveness of releasing *Wolbachia* infected males in controlling *Aedes* mosquito population, with parameters suitable for South Johnstone located in Northern Australia, where mosquito borne diseases frequently outbreak and IIT is allowed to implement [12]. A brief discussion is given in the final section.

2. Model formulation

This section is going to propose a novel modeling framework for mosquito population growth under the influence of seasonal effects, larval competition and proportional releasing strategies of *Wolbachia*-carrying male mosquitoes. The model formulation starts from a seasonal age-structured partial differential equation, which can be further reduced into a system of periodic delay differential equations with periodic delays.

2.1. Seasonal age-structured model with larval competition

Let $u(t,a)$ represent the population density of wild *Wolbachia*-free mosquitoes at time t and chronological age a. In view of seasonal effects, the age threshold differing wild immature and mature mosquitoes is assumed to be time-periodic function with the period T, denoted by $\tau(t)$, which measures the required time for mosquitoes during lumped aquatic stages to develop into adults at time t. In other words, these newly matured adults at time t were developed from immature mosquitoes produced at previous time $t-\tau(t)$. Then the wild mosquito population sizes within aquatic (immature) stage $L(t)$ and adult stage $A(t)$ at time t can be calculated by accumulating the population density between two age thresholds as follows

$$L(t)=\int_0^{\tau(t)} u(t,a)da \qquad \text{and} \qquad A(t)=\int_{\tau(t)}^{a_{\max}} u(t,a)da, \tag{2.1}$$

where $a_{\max}$ is the maximum chronological age of adult mosquitoes, with $a_{\max}-\tau(t)$ ranging from 2 to 4 weeks [57].

Due to confined habitats during the aquatic stage, mosquito larvae may experience strong intraspecific competition through competing food resources with other larvae [42]. By virtue of the ideas proposed in [44, 45], we use the following classic age-structured equation [58–60] with an additional nonlinear term to describe the evolution of larval mosquito population experiencing intra-specific competition

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}\right)u(t,a)=-(m_l(t)+d_l\textstyle\int_0^{\tau(t)} q(a,\bar{a})u(t,\bar{a})d\bar{a})u(t,a), \quad 0<a\le\tau(t),$$

where $m_l(t)$ represents the density-independent natural death rate, which is a positive time-periodic function with period T, while $d_l\int_0^{\tau(t)} q(a,\bar{a})u(t,\bar{a})d\bar{a}$ characterizes the density-dependent self regulation due to competition. Here, d_l measures the intensity of intra-specific larval competition and $q(a,\bar{a})$ is the age dependent weight kernel to describe the integrated effects of competition from different ages of larvae.

Note that the population dynamics of the system largely depend on the kernel function $q(a, \bar{a})$. Under some special forms of $q(a, \bar{a})$, it can be reduced into DDE system. For example, the nonlinear term will become a function of total immature population size, i.e., $f(L(t))$ if $q(a, \bar{a})$ is independent of age a. In this case, the reduced DDE system is analogous to that in [43], where the coupled differential equations with distributed time delay make mathematical analysis fascinating and sometimes very challenging. In the current study, we assume that kernel function $q(a, \bar{a}) = \delta(a - \bar{a})$ takes the form of Dirac delta distributions by assuming that the larvae competition mainly occurs among individuals with same age cohort. We hope this study may motivate future investigations on incorporating more complicated impacts of inter- and intra-specific larval competition [56] on mosquito dynamics. Thus, the evolution of mosquito population density $u(t, a)$ can be described by the following age-structured equations:

$$\begin{cases} \left(\dfrac{\partial}{\partial t} + \dfrac{\partial}{\partial a}\right) u(t,a) = -m_l(t)u(t,a) - d_l u^2(t,a), & 0 < a \leq \tau(t), \\ \left(\dfrac{\partial}{\partial t} + \dfrac{\partial}{\partial a}\right) u(t,a) = -m_a(t)u(t,a), & \tau(t) < a < a_{\max}. \end{cases} \tag{2.2}$$

Positive periodic coefficients $m_l(t)$ and $m_a(t)$ are natural death rates, assumed to have the same period T in view of seasonal effects. The term $d_l u^2(t,a)$ accounts for additional density dependent deaths induced by the intra-specific competition during aquatic stages, taking a quadratic function of the larval population density [44, 45].

2.2. Fecundity under proportional release strategy

Compared with other insect species infected with *Wolbachia*, reproductive manipulations, such as male killing, feminization, or parthenogenesis have not been observed in mosquitoes [61]. Among *Wolbachia* induced effects, only cytoplasmic incompatibility (CI) is considered in our model. It has been observed that the *Wolbachia* strain *w*AlbB can retain very high abilities to induce CI even under extremely high temperature [62, 63]. Thus, it is reasonable to assume the intensity of CI as 100%, that is, a *Wolbachia*-carrying male mated with a wild female mosquito will certainly produce nonviable eggs due to CI. The success of IIT relies on frequently release of *Wolbachia*-carrying males due to their reduced lifespan (≈ 4.5 days). For example, male *Wolbachia*-carrying *Aedes* mosquitoes are released twice a week in Singapore to maintain relatively stable amount between two consecutive releases [64, 65]. Furthermore, daily releases have been conducted in a suppression trial in California, where sufficient amount of *Wolbachia*-infected male mosquitoes can be reared and released per day [55]. In this paper, we take the continuous release under the ideal releasing conditions. It is further assumed that *Wolbachia*-carrying male mosquitoes are deployed continuously under a proportional release strategy, that is, the released amount of male *Wolbachia*-carrying mosquitoes is proportional to the current wild male population and an overflooding ratio p_w is used to quantify the ratio of released *Wolbachia*-carrying males to wild males. The female-male proportion is assumed as $1:1$ since no apparent deviation from this balanced sex-ratio was obtained after long-term censuses of mosquitoes [66]. Then the amount $w(t)$ of released male mosquitoes carrying *Wolbachia* at time t can be characterized as $w(t) = p_w A(t)/2$.

Assume that male mosquitoes infected by *Wolbachia* has the same mating ability as that of wild male mosquitoes. Therefore, the probability of a wild female mosquitoe mating with male *Wolbachia*-carrying mosquitoes at time t can be described as $\dfrac{w(t)}{A(t)/2+w(t)} = \dfrac{p_w}{1+p_w}$. Please note that these mates do not successfully lead to egg production. The probability of a wild female mosquito mating with wild ones is $1-\dfrac{p_w}{1+p_w} = \dfrac{1}{1+p_w}$, with each wild mosquito producing $\alpha(t)$ eggs at time t. Here, the per-capita egg laying rate $\alpha(t)$ is assumed to be periodic with period T. Then the fecundity rate of wild *Wolbachia*-free female mosquitoes (population size $A(t)/2$) under the impact of released *Wolbachia*-infected male mosquitoes at time t, which serves as the boundary condition at $a = 0$ of system (2.2):

$$b(t, A(t), w(t)) = \alpha(t)\frac{1}{(1+p_w)}\frac{A(t)}{2} = \beta_w \alpha(t) A(t) = u(t, 0),$$

where $\beta_w = \dfrac{1}{2(1+p_w)}$ measures the influence of proportional releasing of *Wolbachia*-infected male mosquitoes. The initial age distribution for wild *Wolbachia*-free mosquitoes is shown below:

$$u(0, a) = \phi(a), \quad a \geq 0.$$

Without loss of generality, we assume the following inherent relationship between initial and boundary conditions is satisfied to guarantee the continuity of solutions:

$$u(0, 0) = \phi(0) = \beta_w \alpha(0) A(0) = \beta_w \alpha(0) \int_{\tau(0)}^{a_{\max}} u(0, a) da = \beta_w \alpha(0) \int_{\tau(0)}^{a_{\max}} \phi(a) da.$$

Here, the size of *Wolbachia*-infected male mosquitoes is assumed to be maintained at a given level $w(t)$, and these male mosquitoes are only involved in the reproductive activity of wild mosquitoes and will die at the end. Therefore, there is no need to describe the dynamics of *Wolbachia*-infected male mosquitoes through an additional dynamical process.

2.3. *A delay differential system with periodic delay*

With the aid of system (2.2), we obtain the following equations by differentiating integral terms in (2.1):

$$\begin{cases} \dfrac{dL(t)}{dt} = u(t, 0) - (1 - \tau'(t))u(t, \tau(t)) - m_l(t)L(t) - \displaystyle\int_0^{\tau(t)} d_l u^2(t, a) da, \\ \dfrac{dA(t)}{dt} = (1 - \tau'(t))u(t, \tau(t)) - u(t, a_{\max}) - m_a(t)A(t). \end{cases} \tag{2.3}$$

It is biologically reasonable to assume that $u(t, a_{\max}) = 0$ as no mosquito can survive beyond the maximum lifespan. Besides, $1 - \tau'(t) > 0$ holds to guarantee that the growth proceed along the chronological order and never go back to previous stages. Indeed, the positivity $1 - \tau'(t)$ can be proved [67]. Let $g(t)$ represent seasonal varying growth or development proportion at time t, which measures the speed of progressing through the aquatic stages for wild *Wolbachia*-free mosquitoes [48]. Thus, the accumulative developmental proportion within the time period $[t-\tau(t), t]$ should be unity when the immature mosquitoes become maturation at time t, that is, $\int_{t-\tau(t)}^{t} g(r)dr = 1$. It then follows from the differentiation with respect to t that

$$1-\tau'(t) = \frac{g(t)}{g(t-\tau(t))} > 0.$$

To obtain the closed form of system (2.3), it is imperative to determine $\int_0^{\tau(t)} u^2(t,a)da$ and $u(t,\tau(t))$, which is calculated by integration along characteristics. Set $\hat{\tau} = \max_{t\in[0,T]}\{\tau(t)\}$. For any $s \geq -\hat{\tau}$ and fixed t_0, a_0, let $\rho(s) = u(t_0+s, a_0+s)$ and $\bar{m}_l(s) = m_l(t_0+s)$. In the case of $0 < a_0 + s \leq \tau(t)$, we have

$$\begin{aligned}\frac{d\rho(s)}{ds} &= \left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) u(t_0+s, a_0+s) \\ &= -m_l(t_0+s)u(t_0+s,a_0+s) - d_l u^2(t_0+s,a_0+s) \\ &= -\bar{m}_l(s)\rho(s) - d_l\rho^2(s).\end{aligned}$$

By employing the method of solving the first order Bernoulli differential equation, solutions of the above system is given as follows:

$$\rho(s) = \frac{\rho(0)e^{-\int_0^s \bar{m}_l(r)dr}}{1+\rho(0)\int_0^s d_l e^{-\int_0^r \bar{m}_l(h)dh}dr},$$

which is equivalent to

$$u(t_0+s, a_0+s) = \frac{u(t_0,a_0)e^{-\int_0^s m_l(t_0+r)dr}}{1+u(t_0,a_0)\int_0^s d_l e^{-\int_0^r m_l(t_0+h)dh}dr}.$$

Two different formulae of $u(t,a)$ can be obtained as follows by assigning different values to t_0, a_0, and s:

$$u(t,a) = \begin{cases} \dfrac{\phi(a-t)e^{-\int_0^t m_l(a-t+r)dr}}{1+\phi(a-t)\int_0^t d_l e^{-\int_0^r m_l(a-t+h)dh}dr}, & t < a, t_0 = 0, a_0 = a-t, s = t, \\ \dfrac{\beta_w\alpha(t-a)A(t-a)e^{-\int_0^a m_l(t-a+r)dr}}{1+\beta_w\alpha(t-a)A(t-a)\int_0^a d_l e^{-\int_0^r m_l(t-a+h)dh}dr}, & t \geq a, a_0 = 0, t_0 = t-a, s = a. \end{cases}$$

Since we are focusing on the long-term dynamics of population size, the formulation of $u(t,a)$ in the case of $t \geq a$ is investigated in what follows. Thus, the population growth of wild mosquito population under the impact of released *Wolbachia*-infected male mosquitoes can be described as the following delay differential equations with periodic delays:

$$\begin{cases} \dfrac{dL(t)}{dt} = & \beta_w\alpha(t)A(t) - m_l(t)L(t) \\ & -(1-\tau'(t))\dfrac{\beta_w\alpha(t-\tau(t))A(t-\tau(t))e^{-\int_{t-\tau(t)}^{t} m_l(r)dr}}{1+\beta_w\alpha(t-\tau(t))A(t-\tau(t))\int_{t-\tau(t)}^{t} d_l e^{-\int_{t-\tau(t)}^{r} m_l(h)dh}dr} \\ & -d_l\int_{t-\tau(t)}^{t} \dfrac{[\beta_w\alpha(\eta)A(\eta)e^{-\int_{\eta}^{t} m_l(r)dr}]^2}{[1+\beta_w\alpha(\eta)A(\eta)\int_{\eta}^{t} d_l e^{-\int_{\eta}^{r} m_l(h)dh}dr]^2}d\eta, \\ \dfrac{dA(t)}{dt} = & (1-\tau'(t))\dfrac{\beta_w\alpha(t-\tau(t))A(t-\tau(t))e^{-\int_{t-\tau(t)}^{t} m_l(r)dr}}{1+\beta_w\alpha(t-\tau(t))A(t-\tau(t))\int_{t-\tau(t)}^{t} d_l e^{-\int_{t-\tau(t)}^{r} m_l(h)dh}dr} - m_a(t)A(t), \end{cases} \tag{2.4}$$

where $\beta_w = \dfrac{1}{2(1+p_w)}$, all parameters and their meanings are listed in Table 1.

Table 1: Description of parameters in model (2.4).

Parameters	Description
$\alpha(t)$	Egg laying rate
$m_l(t)$	Natural death rate during aquatic stages
$m_a(t)$	Natural death rate during adult stage
$\tau(t)$	Developmental duration for immature mosquitoes to develop into adults
p_m	Overflooding ratio, the ratio of released *Wolbachia* infected males to wild-type males
d_l	Intensity of larval competition

3. Theoretical analysis of the model

It is easy to see that the variable $L(t)$ related to immature mosquitoes is not involved in the equation for the other variable $A(t)$ and $L(t)$ can be determined by the following integral form

$$\begin{aligned} L(t) = \int_0^{\tau(t)} u(t,a)da &= \int_0^{\tau(t)} \frac{\beta_w\alpha(t-a)A(t-a)e^{-\int_0^a m_l(t-a+r)dr}}{1+\beta_w\alpha(t-a)A(t-a)\int_0^a d_l e^{-\int_0^r m_l(t-a+h)dh}dr}da \\ &\xlongequal{t-a=\eta} \int_{t-\tau(t)}^{t} \frac{\beta_w\alpha(\eta)A(\eta)e^{-\int_0^{t-\eta} m_l(\eta+r)dr}}{1+\beta_w\alpha(\eta)A(\eta)\int_0^{t-\eta} d_l e^{-\int_0^r m_l(\eta+h)dh}dr}d\eta \\ &\xlongequal[\eta+r=s]{\eta+h=\theta} \int_{t-\tau(t)}^{t} \frac{\beta_w\alpha(\eta)A(\eta)e^{-\int_\eta^t m_l(s)ds}}{1+\beta_w\alpha(\eta)A(\eta)\int_\eta^t d_l e^{-\int_\eta^s m_l(\theta)d\theta}dr}d\eta. \end{aligned} \tag{3.1}$$

It is sufficient to investigate the dynamics of $A(t)$ first, which is given by the second equation of system (2.4) and copied as follows for easy reference

$$\frac{dA(t)}{dt}=(1-\tau'(t))\frac{\beta_w\alpha(t-\tau(t))A(t-\tau(t))e^{-\int_{t-\tau(t)}^{t}m_l(r)dr}}{1+\beta_w\alpha(t-\tau(t))A(t-\tau(t))\int_{t-\tau(t)}^{t}d_le^{-\int_{t-\tau(t)}^{r}m_l(h)dh}dr}-m_a(t)A(t).\tag{3.2}$$

3.1. Global existence and uniqueness of solutions

In order to choose feasible state space for the evolution of solutions, the maximum value of the periodic function $\tau(t)$ should be identified as $\hat{\tau}=\max_{t\in[0,T]}\{\tau(t)\}$ and the state space can be specified as $\mathbf{X}:=C([-\hat{\tau},0],\mathbb{R})$, which is the Banach space of continuous functions equipped with the usual maximum norm. Through shifting the initial time, we assume $\tau(0)=\hat{\tau}$, which makes $\mathbf{X}=C([-\tau(0),0],\mathbb{R})$. Define $\mathbf{X}_+:=C([-\hat{\tau},0],\mathbb{R}_+)$, then $(\mathbf{X},\mathbf{X}_+)$ is an ordered Banach space, the partial order of which is induced by the positive cone $\mathbf{X}_+$. Given a continuous function $v(t):[-\hat{\tau},\sigma)\to\mathbf{X}$ for $\sigma>0$, denote $v_t\in\mathbf{X}$ by $v_t(\theta)=v(t+\theta)$, for all $\theta\in[-\hat{\tau},0]$ and $t\in[0,\sigma)$. For any $\phi\in\mathbf{X}$, define $f(t,\phi)$ as

$$f(t,\phi)=(1-\tau'(t))\frac{\beta_w\alpha(t-\tau(t))\phi(-\tau(t))e^{-\int_{t-\tau(t)}^{t}m_l(r)dr}}{1+\beta_w\alpha(t-\tau(t))\phi(-\tau(t))\int_{t-\tau(t)}^{t}d_le^{-\int_{t-\tau(t)}^{r}m_l(h)dh}dr}-m_a(t)\phi(0).$$

Then it is easy to check $f(t+T,\phi)=f(t,\phi)$. Thus, system (3.2) is a T-periodic functional differential system. For any given continuous T-periodic function $r(t)$, following notations for global maximum and minimum values during one period are introduced

$$\hat{r}=\max_{t\in[0,T]}\{r(t)\}\quad\text{and}\quad\bar{r}=\min_{t\in[0,T]}\{r(t)\}.$$

In view of the fact that system (3.2) depicts the evolution of mosquito population, it is imperative to verify its biological rationality, that is, the nonnegativity and boundedness of the solutions, which is established in the next statement.

Theorem 3.1. *For any $\phi\in\mathbf{X}_+$, system (3.2) admits a unique nonnegative and bounded solution $A(t;\phi)$ with $A_0=\phi$ on $[0,+\infty)$. Moreover, system (3.2) generates a T-periodic semiflow $\Phi_t=A_t(\cdot):\mathbf{X}_+\to\mathbf{X}_+$, i.e. $\Phi_t(\phi)(\theta)=A(t+\theta;\phi)$, $\forall t\geq 0,\theta\in[-\hat{\tau},0]$.*

Proof. Note that $F(t,\phi)$ is locally Lipschitz continuous in ϕ in any compact subset of $\mathbf{X}_+$, which indicates that for any $\phi\in\mathbf{X}_+$, system (3.2) admits a unique non-continuable solution $A(t;\phi)$ with $A_0=\phi$ in its maximal interval of existence [68]. It is easy to check that $f(t,\phi)\geq 0$ whenever $\phi(0)=0$, then $A(t;\phi)\geq 0$ on its interval of existence through the comparison arguments in [69, Theorem 5.2.1 and Remark 5.2.1]. Therefore, the following inequality holds

$$\frac{dA(t)}{dt}\leq(1-\tau'(t))\frac{e^{-\int_{t-\tau(t)}^{t}m_l(r)dr}}{\int_{t-\tau(t)}^{t}d_le^{-\int_{t-\tau(t)}^{r}m_l(h)dh}dr}-m_a(t)A(t).$$

Set

$$\tilde{A}=\max_{t\in[0,T]}\left\{(1-\tau'(t))\frac{e^{-\int_{t-\tau(t)}^{t}m_l(r)dr}}{m_a(t)\int_{t-\tau(t)}^{t}d_l e^{-\int_{t-\tau(t)}^{r}m_l(h)dh}dr}\right\}.$$

Then for any initial function satisfying $\psi(\theta)\le\lambda\tilde{A}$ with $\lambda\ge 1$, $\forall\theta\in[-\hat{\tau},0]$, it is easy to check that $f(t,\psi)\le 0$ whenever $\psi(0)=\lambda\tilde{A}$. Therefore, it follows from [69, Theorem 5.2.1 and Remark 5.2.1] that $A(t;\psi)\le\lambda\tilde{A}$. Hence, $[0,\lambda\tilde{A}]$ is positively invariant for system (3.2). The positivity and boundedness of solutions is then obtained in $\mathbf{X}_+$. Since for any $\phi\in\mathbf{X}_+$, there exists $\lambda>1$ such that $\phi\in[0,\lambda\tilde{A}]$, the unique solution $A(t;\phi)$ globally exists on $[0,+\infty)$. Furthermore, Φ_t is a T-periodic semiflow based on similar arguments in [67, Lemma 3.5]. □

The T-periodic semiflow Φ_t can be shown to be strongly monotone and strictly subhomogeneous in the subsequent lemmas.

Lemma 3.2. *For any ϕ and ψ in $\mathbf{X}_+$ with $\phi>\psi$ (i.e. $\phi\ge\psi$ but $\phi\ne\psi$), the solutions $u(t;\phi)$ and $v(t;\psi)$ of system (3.2) with $u(\theta)=\phi(\theta)$ and $v(\theta)=\psi(\theta)$, for all $\theta\in[-\hat{\tau},0]$ respectively, satisfy that $u(t;\phi)>v(t;\psi)$ for all $t>\hat{\tau}$ and hence $\Phi_t(\phi)\gg\Phi_t(\psi)$ in $\mathbf{X}$ for all $t>2\hat{\tau}$.*

Proof. Note that $\dfrac{\beta_w\alpha(s-\tau(s))ze^{-\int_{s-\tau(s)}^{s}m_l(r)dr}}{1+\beta_w\alpha(s-\tau(s))z\int_{s-\tau(s)}^{s}d_l e^{-\int_{s-\tau(s)}^{r}m_l(h)dh}}$ is a strictly increasing function of z for $z\in[0,\infty)$. For any ϕ, $\psi\in\mathcal{X}_+$ with $\phi>\psi$, by virtue of comparison theorem for cooperative systems [69], we obtain $u(t;\phi)\ge v(t;\psi)$ for all $t\ge 0$.

Let $g_h(t,z)=-m_a(t)z+hz$ with parameter h, then both $u(t;\phi)$ and $v(t;\psi)$ satisfy the following integral form:

$$\begin{aligned}z(t)=&e^{-ht}z(0)+\int_0^t e^{-h(t-s)}g_h(s,z(s))ds\\&+\int_0^t e^{-h(t-s)}(1-\tau'(s))\frac{\beta_w\alpha(s-\tau(s))z(s-\tau(s))e^{-\int_{s-\tau(s)}^{s}m_l(r)dr}}{1+\beta_w\alpha(s-\tau(s))z(s-\tau(s))\int_{s-\tau(s)}^{s}d_l e^{-\int_{s-\tau(s)}^{r}m_l(h)dh}dr}ds\end{aligned}\tag{3.3}$$

with $z(\theta)=\phi(\theta)$ and $z(\theta)=\psi(\theta)$ respectively. Choose any large number $h>\max_{t\in[0,T]}\{m_a(t)\}$, then $g_h(t,z)$ is strictly increasing on $z\in[0,\infty)$. Assume that $u(t;\phi)=v(t;\psi)$ for all $t\in[0,\hat{\tau}]$, then the strictly monotonicity of all following terms on $z\in[0,\infty)$

$$e^{-ht}z,\ g_h(s,z),\frac{\beta_w\alpha(s-\tau(s))ze^{-\int_{s-\tau(s)}^{s}m_l(r)dr}}{1+\beta_w\alpha(s-\tau(s))z\int_{s-\tau(s)}^{s}d_l e^{-\int_{s-\tau(s)}^{r}m_l(h)dh}}$$

in the above integral form (3.3) implies that $\phi\equiv\psi$, a contradiction. Therefore, there is $t_0\in[0,\hat{\tau}]$ such that $u(t_0;\phi)>v(t_0;\psi)$. Moreover, (3.3) also implies that $u(t;\phi)>v(t;\psi)$ for all $t\ge t_0$. As a consequence, the strong monotonicity of the periodic semiflow Φ_t holds whenever $t>2\hat{\tau}$.

□

The coming result shows the strict subhomogeneity property of the periodic semiflow Φ_t.

Lemma 3.3. *$\Phi_t(\phi) : \mathbf{X}_+ \to \mathbf{X}_+$ is strictly subhomogeneous whenever $t > 2\hat{\tau}$, that is, given any $\phi \gg 0$ in $\mathbf{X}_+$ and $\lambda \in (0,1)$, $u(t;\lambda\phi) > \lambda u(t;\phi)$ holds for all $t > \hat{\tau}$, and hence $\Phi_T^n(\lambda\phi) \gg \lambda\Phi_T^n(\phi)$ in $\mathbf{X}_+$ holds for all $n \in \mathbb{N}_+$ satisfying $nT > 2\hat{\tau}$.*

Proof. Let $u(t;\phi)$ and $u(t;\lambda\phi)$ be the solution of system (3.2) with initial condition $\phi(\theta) > 0$ and $\lambda\phi(\theta) > 0$ for all $\theta \in [-\hat{\tau}, 0]$, respectively. Then the integral form (3.3) indicates $u(t;\phi) > 0$ and $u(t;\lambda\phi) > 0$ for all $t \geq 0$. We first claim that $\lambda u(t;\phi) < u(t;\lambda\phi)$ for all $0 < t < \bar{\tau}$. Note that

$$\begin{aligned}
& \left.\frac{d(\lambda u(t;\phi))}{dt}\right|_{t=0} \\
= & \ (1-\tau'(0))\frac{\beta_w\alpha(-\hat{\tau})(\lambda\phi(-\hat{\tau}))e^{-\int_{-\hat{\tau}}^0 m_l(r)dr}}{1+\beta_w\alpha(-\hat{\tau})\phi(-\hat{\tau})\int_{-\hat{\tau}}^0 d_l e^{-\int_{-\hat{\tau}}^r m_l(h)dh}dr} - m_a(0)(\lambda\phi(0)) \\
< & \ (1-\tau'(0))\frac{\beta_w\alpha(-\hat{\tau})(\lambda\phi(-\hat{\tau}))e^{-\int_{-\hat{\tau}}^0 m_l(r)dr}}{1+\beta_w\alpha(-\hat{\tau})(\lambda\phi(-\hat{\tau}))\int_{-\hat{\tau}}^0 d_l e^{-\int_{-\hat{\tau}}^r m_l(h)dh}dr} - m_a(0)(\lambda\phi(0)) \\
= & \left.\frac{d(u(t;\lambda\phi))}{dt}\right|_{t=0}.
\end{aligned}$$

Besides, $\lambda u(0;\phi) = u(0;\lambda\phi) > 0$ implies the existence of an $\epsilon \in (0,\bar{\tau})$ such that $0 < \lambda u(t;\phi) < u(t;\lambda\phi)$ for all $t \in (0,\epsilon)$. Next, we show $\lambda u(t;\phi) < u(t;\lambda\phi)$ for all $t \in (0,\bar{\tau}]$ through arguments of contradiction. Assume there is some $t_0 \in (0,\bar{\tau}]$ such that $\lambda u(t;\phi) < u(t;\lambda\phi)$ holds for all $0 < t < t_0$ but $\lambda u(t_0;\phi) = u(t_0;\lambda\phi)$. Then we must have $\lambda u'(t_0;\phi) \geq u'(t_0;\lambda\phi)$. However,

$$\begin{aligned}
& \left.\frac{d(\lambda u(t;\phi))}{dt}\right|_{t=t_0} \\
= & \ (1-\tau'(t_0))\frac{\beta_w\alpha(t_0-\tau(t_0))(\lambda\phi(t_0-\tau(t_0)))e^{-\int_{t_0-\tau(t_0)}^{t_0} m_l(r)dr}}{1+\beta_w\alpha(t_0-\tau(t_0))\phi(t_0-\tau(t_0))\int_{t_0-\tau(t_0)}^{t_0} d_l e^{-\int_{t_0-\tau(t_0)}^r m_l(h)dh}dr} - m_a(t_0)(\lambda\phi(t_0)) \\
< & \ (1-\tau'(t_0))\frac{\beta_w\alpha(t_0-\tau(t_0))(\lambda\phi(t_0-\tau(t_0)))e^{-\int_{t_0-\tau(t_0)}^{t_0} m_l(r)dr}}{1+\beta_w\alpha(t_0-\tau(t_0))(\lambda\phi(t_0-\tau(t_0)))\int_{t_0-\tau(t_0)}^{t_0} d_l e^{-\int_{t_0-\tau(t_0)}^r m_l(h)dh}dr} - m_a(t_0)(\lambda\phi(t_0)) \\
= & \left.\frac{d(u(t;\lambda\phi))}{dt}\right|_{t=t_0},
\end{aligned}$$

which is a contradiction. Thus, $\lambda u(t;\phi) < u(t;\lambda\phi)$ holds for all $t \in (0,\bar{\tau}]$. Therefore, $\lambda u(t;\phi) < u(t;\lambda\phi)$ holds for all $t \in (n\bar{\tau},(n+1)\bar{\tau}]$ with $n \in \mathbb{N}$ by applying similar statements repeatedly in each interval. Hence, we conclude that $\lambda u(t;\phi) < u(t;\lambda\phi)$ for all $t > \hat{\tau}$ and $\Phi_T^n(\lambda\phi) \gg \lambda\Phi_T^n(\phi)$ holds for all $n \in \mathbb{N}_+$ when $nT > 2\hat{\tau}$.

□

3.2. Basic offspring number and threshold dynamics

In this subsection, the basic offspring number $\mathcal{R}_0$ is first formulated by virtue of recent theory related to periodic functional system with periodic time delays developed in [70].

The global dynamics of system (3.2) in terms of $\mathcal{R}_0$ is then established based on the theory of monotone and subhomogeneous semiflows [71]. The linearized system of (3.2) at the population extinction equilibrium is shown as follows:

$$\frac{dA(t)}{dt} = b_a(t)A(t-\tau(t)) - m_a(t)A(t), \tag{3.4}$$

where $b_a(t) = (1-\tau'(t))\beta_w\alpha(t-\tau(t))e^{-\int_{t-\tau(t)}^{t} m_l(r)dr}$.

For any $\phi \in \mathbf{X}_+$, let $F(t)\phi = b_a(t)\phi(-\tau(t))$ represent the recruitment of adult mosquitoes. The survival probability $\mathcal{H}(t,s)$ of adult mosquitoes from time instant s to t is determined by the following linear system

$$\frac{du(t)}{dt} = -m_a(t)u(t),$$

then, we have $\mathcal{H}(t,s) = e^{-\int_s^t m_a(\eta)d\eta}$.

Set the ordered Banach space of all T-periodic continuous functions from $\mathbb{R}$ to $\mathbb{R}$ as C_T, the norm of which is the usual maximum norm. The positive cone is defined as $C_T^+ := \{\psi \in C_T : \psi(t) \geq 0, \forall t \in \mathbb{R}\}$. Given $\psi(s) \in C_T^+$ as the initial distribution of adult mosquitoes at time s, then $F(t-s)\psi(t-s)$ represents the distribution of newly recruited adult mosquitoes at time $t-s$ with $t \geq s \geq 0$. Then, $\mathcal{H}(t,t-s)F(t-s)\psi_{t-s}$ is the distribution of those newly matured adult mosquitoes at time $t-s$ and still survive to time t ($t \geq s$). Thus, the following integral form shows the distribution of accumulative newly recruited adult mosquitoes at time t, who were produced by adult female mosquitoes borne at all previous time to t:

$$\begin{aligned}&\int_0^\infty \mathcal{H}(t,t-s)F(t-s)\psi_{t-s}ds\\ =&\int_0^\infty e^{-\int_{t-s}^{t} m_a(\eta)d\eta}(1-\tau'(t-s))\beta_w\alpha(t-s-\tau(t-s)) \times e^{-\int_{t-s-\tau(t-s)}^{t-s} m_l(r)dr}\psi(t-s+\cdot)ds.\end{aligned}$$

The next generation operator $\mathcal{L} : C_T \to C_T$ is

$$(\mathcal{L}\psi)(t) = \int_0^\infty \mathcal{H}(t,t-s)F(t-s)\psi(t-s+\cdot)ds, \forall t \in \mathbb{R}, \psi \in C_T.$$

Hence, the basic offspring number R_0 is defined as $\mathcal{R}_0 := r(\mathcal{L})$ with $r(\mathcal{L})$ being the spectral radius of the next generation operator $\mathcal{L}$. Due to the complicated form of the basic offspring number R_0, it is difficult to determine the explicit relationship between the IIT-related parameter p_w and R_0. However, the derivation of R_0 implies that the variation of p_w has a huge negative impact on the value of R_0, which is illustrated in Figure 3 in the numerical simulation.

Let $\Psi(t)$ represent the solution map of the linear periodic system (3.4) on $\mathbf{X}$. For given $\phi \in \mathbf{X}$, let $v(t;\phi)$ be the unique solution of system (3.4) with initial condition $v_0 = \phi$. Then, we have $\Psi(t)\phi = v_t(\phi)$. In light of [70, Theorem 3.7], we can prove that the stability of the zero solution of system (3.4) is determined by the threshold value $\mathcal{R}_0 - 1$.

Lemma 3.4. *$\mathcal{R}_0 - 1$ has the same sign as $r(\Psi(T)) - 1$.*

Recall that the solution map of system (3.2) Φ_t is strongly monotone and strictly subhomogeneous, which have been shown in Lemmas 3.2 and 3.3. Then, the next result on threshold dynamics of system (3.2) holds.

Theorem 3.5. *The following statements are valid:*

(i) If $\mathcal{R}_0 \leq 1$, then the zero solution is globally attractive for all solutions of system (3.2)*.*

(ii) If $\mathcal{R}_0 > 1$, then system (3.2) *admits a unique T-periodic solution $A^*(t)$, which is globally asymptotically stable in $\boldsymbol{X}_+ \backslash \{0\}$.*

Proof. Fix an integer n_0 such that $n_0 T > 2\hat{\tau}$. Φ_t can be proved as a $n_0 T$-periodic semiflow on $\mathbf{X}_+$ by applying similar statements in the proof of [67, Lemma 3.5]. It then follows from Lemmas 3.2 and 3.3 that $\Phi_{n_0 T}$ is a strongly monotone and strictly subhomogeneous map on $\mathbf{X}_+$. By virtue of [71, Theorem 2.3.4], the following threshold results for the map $\Phi_{n_0 T}$ hold:

(1) If $r(D(\Phi_{n_0 T})) \leq 1$, then the zero solution is globally asymptotically stable for system (3.2) in $\mathbf{X}_+$.

(2) If $r(D(\Phi_{n_0 T})) > 1$, then system (3.2) admits a unique positive $n_0 T$-periodic solution $A^*(t)$, which is globally asymptotically stable for system (3.2) in $\mathbf{X}_+ \backslash 0$.

Note that $r(D(\Phi_{n_0 T})) = (r(\Psi(n_0 T))) = (r(\Psi(T)))^{n_0}$. It follows from Lemma 3.4 that two values $R_0 - 1$ and $r(D(\Phi_{n_0 T})) - 1$ have the same sign, that is $sign(R_0 - 1) = sign(r(D(\Phi_{n_0 T})) - 1)$. To complete the proof, we need to further show the unique positive solution A^* is also T-periodic. Indeed,

$$\Phi_T^{n_0}(\Phi_T \psi^*) = \Phi_T(\Phi_T^{n_0} \psi^*) = \Phi_T(\Phi_{n_0 T} \psi^*) = \Phi_T(\psi^*),$$

where $\psi^*(s) = A^*(s)$ for all $s \in [-\tau(0), 0]$ guaranteeing $\Phi_{n_0 T} \psi^* = \psi^*$. The uniqueness of the positive fixed point of $\Phi_T^{n_0} = \Phi_{n_0 T}$ indicates that $\Phi_T \psi^* = \psi^*$. Thus, $A^*(t)$ is a T-periodic solution of system (3.2). □

It follows from (3.1) that $L(t)$ can be represented as the equivalent integral form:

$$L(t) = \int_{t-\tau(t)}^{t} \frac{\beta_w \alpha(\eta) A(\eta) e^{-\int_\eta^t m_l(s)ds}}{1 + \beta_w \alpha(\eta) A(\eta) \int_\eta^t d_l e^{-\int_\eta^s m_l(\theta)d\theta} dr} d\eta.$$

Based on the integral form, the dynamics of the other variable $L(t)$ are easy to deduce from the global asymptotic property of $A(t)$ when $R_0 > 1$, that is,

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

where $L^*(t) = \int_{t-\tau(t)}^{t} \dfrac{\beta_w \alpha(\eta) A^*(\eta) e^{-\int_\eta^t m_l(s)ds}}{1+\beta_w\alpha(\eta)A^*(\eta)\int_\eta^t d_l e^{-\int_\eta^s m_l(\theta)d\theta}dr} d\eta$ is a positive T-periodic function. Applying similar statements, we can obtain the dynamics of $L(t)$ under the scenario of $R_0 \leq 1$. As a consequence, we conclude the global attractivity of system (2.4), shown in the following theorem.

Theorem 3.6. *The following statements are valid:*

(i) If $\mathcal{R}_0 \leq 1$, then the population extinction equilibrium $(0,0)$ *is globally attractive for all solutions of system* (2.4)*.*

(ii) If $\mathcal{R}_0 > 1$, then system (2.4) *admits a unique T-periodic solution* $(L^*(t), A^*(t))$*, which is globally attractive to all nontrivial solutions.*

4. Numerical analysis

In this section, numerical simulations are performed. Continuous repeated releases are assumed to be conducted to a hypothetical isolated *Wolbachia*-free mosquito population inhabiting in South Johnstone, Northern Australia (NA), where the *Aedes-Wolbachia* based population-suppression experiment was allowed to carry out [12]. The intention of our simulation is to not only validate the theoretical results but also investigate the reduction effects of released male *Wolbachia*-carrying mosquitoes under consideration of seasonal factors and larval competition.

4.1. Estimation of parameters

The estimation of two time-independent parameters (d_l and p_w) is a challenging problem since there are very few related references. In this paper, these two parameters are assumed to be variable, the variation of which will uncover the impact of larval competition and released *Wolbachia*-carrying male mosquitoes in further numerical analysis. In particular, the intensity of larval competition is closely related to the carrying capacity of environment. Here, we assume that the carrying capacity of mosquitoes in South Johnstone ranges from 100 to 10000. Hence, the value of larval competition rate d_l varies within the range of $[1/10^4, 1/10^2]$. Other parameters in our model are varying periodically with time. It is imperative to determine the time-periodic parameters before carrying out numerical analysis. The birth rate, mortality rate and developmental duration are all assumed to be determined by temperature conditions to incorporate the seasonal effects. In order to determine time periodic parameters, the monthly average temperature data of South Johnstone (see the table in Figure 1) is downloaded from Australian government portal [72]. With the aid of Curve Fitting Toolbox in Matlab, the time-periodic function $P(t)$ is fitted to approximately capture the evolution of annual temperature in South Johnstone (see Figure 1).

The relations between temperature and temperature-dependent parametric functions are then derived from the temperature-controlled experiments on *Aedes aegypti* [73, 74]. Since the egg, larval and pupal stages are merged into one immature stage in this paper, temperature-dependent duration function is fitted with full development duration data provided in [74]. The form of temperature-dependent birth and death rates are the same as that in [50]. Detailed information of all parameters are shown in Table 2. The red dashed curves in Figure 2 show how seasonal parameters vary with temperatures, while the blue solid curves uncover yearly evolutionary pattern of these time-periodic parameters. Developmental time during joint aquatic stages $\tau(t)$ shortens to a minimum value when the temperature increases to around 30°C and lengthens slightly thereafter. Unique maximum developmental duration occurs in the winter season when the temperature becomes low. Compared with developmental duration $\tau(t)$, per-capita egg laying rate $\alpha(t)$ exhibits opposite changing trend, the fluctuation pattern of which is similar as that of temperature (shown in Figure 1). The mortality rate during joint aquatic ($m_l(t)$) and adult ($m_a(t)$) stage show disparate variational tendency from the temperature variation. More valleys and peaks appear in the seasonal pattern of mortality rate, which indicates that it is worth exploring more accurate relations between temperatures and time-varying parameters.

Month	Temperature (°C)
January	31.2
February	30.8
March	29.9
April	28.3
May	26.3
June	24.4
July	24
August	25.2
September	27.1
October	29
November	30.5
December	31.2

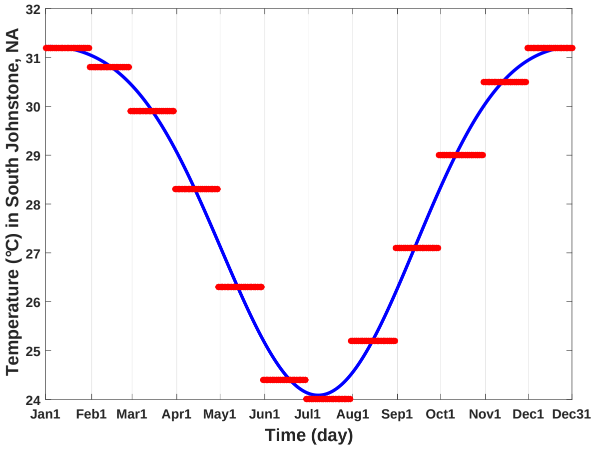


Figure 1: Monthly temperature on average and fitted curves of the yearly temperature in South Johnstone, Northern Australia (NA)

4.2. Effects of seasonality

In this subsection, the effects of temperature on mosquito populations are explored by comparing the basic offspring number R_0 with the case that seasonality is not taken into account. By virtue of the method provided in [75], the time-averaged value of any continuous periodic function $f(t)$ is denoted by $[f]$ and calculated as follows:

$$[f] := \frac{1}{T}\int_0^T f(t)dt.$$

We then obtain the time-averaged values for all periodic parameters: $[\tau] = 6.5254$, $[m_l] = 0.0278$, $[m_a] = 0.0147$ and $[\alpha] = 3.893$, which are used as the baseline parameter values when seasonal factors are not considered.

Based on the estimated time dependent and time-averaged parameters, the basic offspring numbers R_0 for both cases are calculated by using the bisection method provided in Lemma

Table 2: Temperature independent parameters and temperature dependent seasonal functions.

Name	Formulations/Ranges	Resources
Temperature function, $P(t)$	$P(t) = 28.18 + 3.55\cos(2\pi t/365) + 0.3554\sin(2\pi t/365) - 0.5091\cos(4\pi t/365) - 0.1388\sin(4\pi t/365)$	Fitted
Egg laying rate, $\alpha(P)$	$\alpha(P) = -5.4 + 1.8P - 0.2124P^2 + 0.01015P^3 - 1.515 \times 10^{-4}P^4$	[50, 74]
Death rate during aquatic stages, $m_l(P)$	$m_l(P) = 2.13 - 0.3797P + 0.02457P^2 - 6.778 \times 10^{-4}P^3 + 6.794 \times 10^{-6}P^4$	[50, 73]
Death rate during adult stage, $m_a(P)$	$m_a(P) = 0.8692 - 0.159P + 0.01116P^2 - 3.408 \times 10^{-4}P^3 + 3.809 \times 10^{-6}P^4$	[50, 73]
Developmental duration, $\tau(P)$	$\tau(P) = -0.001117P^4 + 0.1156P^3 - 4.275P^2 + 64.97P - 306.6$	[74]
Overflooding ratio, p_m	$[0, +\infty)$	Assumed
Intensity of larval competition, d_l	$[1/10^4, 1/10^2]$	Assumed

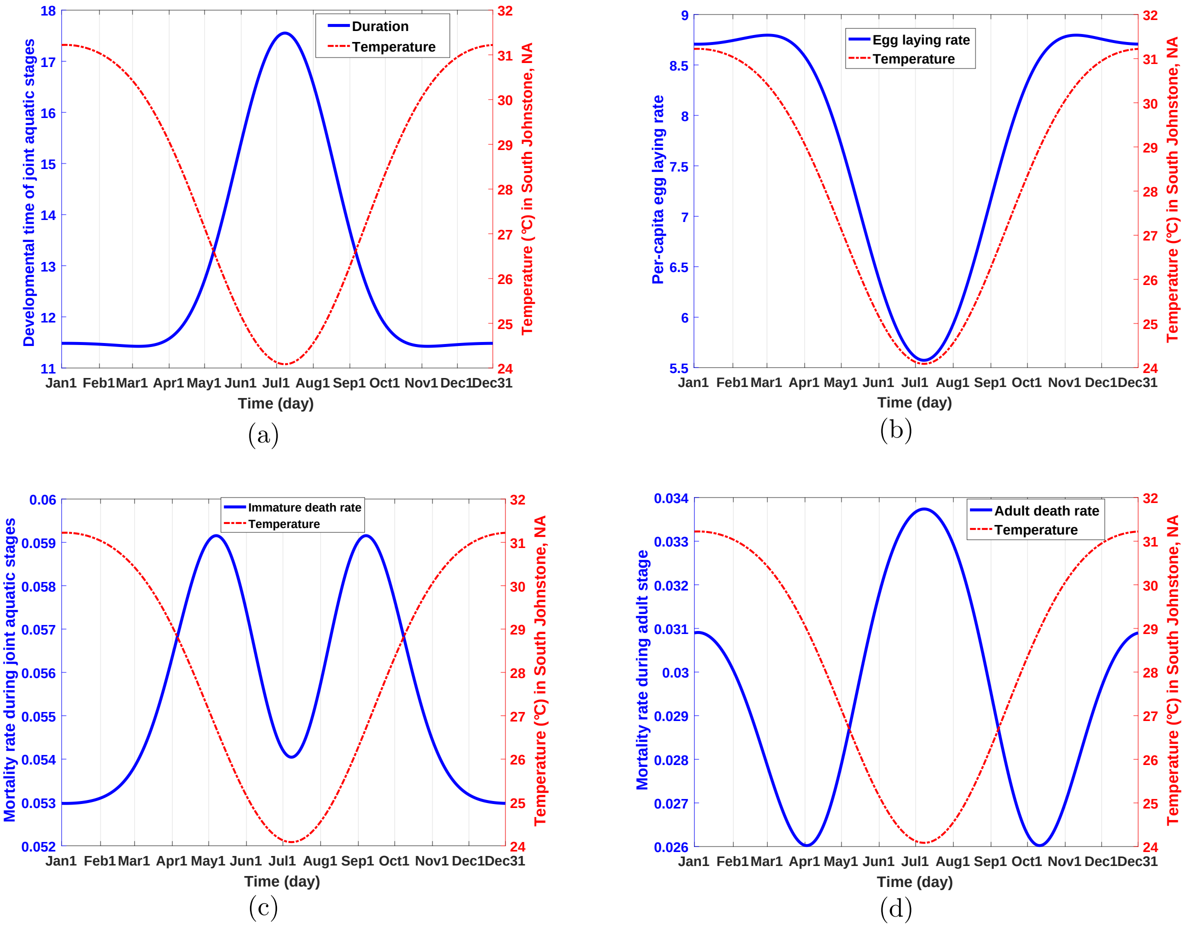


Figure 2: Fitted curves of seasonal time-periodic parameters. The blue solid curves depict how temperature dependent parameters evolve over time seasonally, with values indicated in y-axis on the left. The red dashed curves describe how temperature varies with time, with values indicated in the red y-axis on the right.

2.5 in [70] once the overflooding ratio p_w is fixed. Figure 3 implies that the variation of the overflooding ratio p_w has a huge negative impact on the value of R_0 for both cases. The basic offspring number R_0 is quite big when control strategies are not implemented (i.e. $p_w = 0$). It then shows an apparent decline with the increase of p_w. Compared with R_0 calculated based on the seasonal model, evident overestimate of the basic offspring number can be seen from Figure 3 when seasonal effects are ignored.

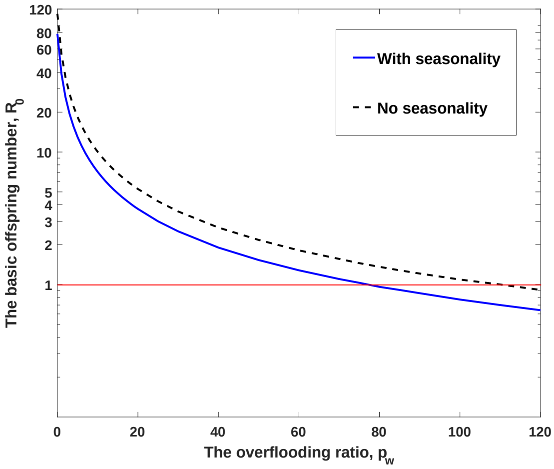


Figure 3: The basic offspring number R_0 varies with the overflooding ratio p_w under two scenarios. In order to highlight the threshold value of p_w when $R_0 = 1$, the vertical y-axis is labeled according to a logarithmic scale.

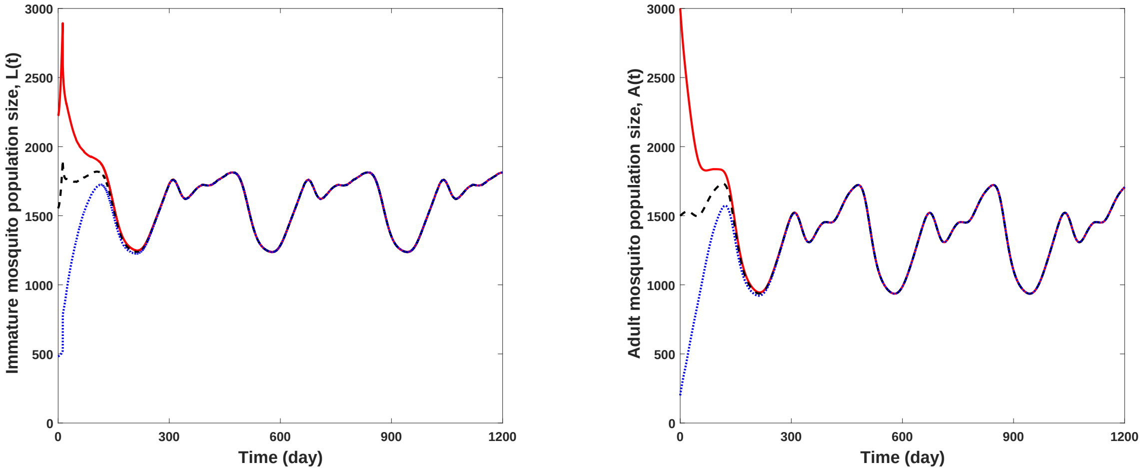
4.3. Threshold dynamics

Fix the larval density dependent death rate d_l as $d_l = 1/10^3$, solutions of the model can then be calculated numerically. Under two different levels of R_0, the long term dynamics of $L(t)$ and $A(t)$ with three different initial conditions are shown in Figure 4. Solutions with various initial conditions all approach to zero if $R_0 < 1$ and to a stable periodic solution when $R_0 > 1$. This result confirms our theoretical results about long term threshold dynamics in Theorem 3.6.

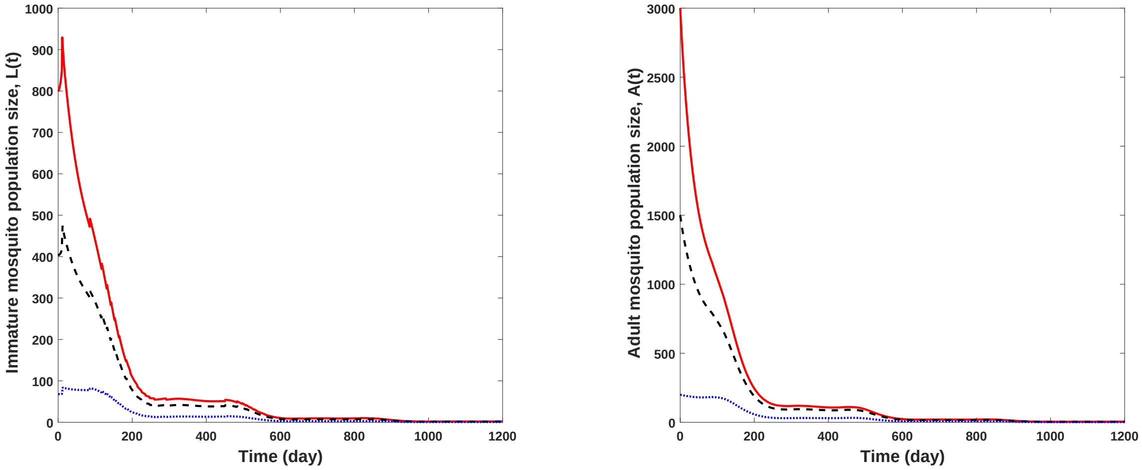
In the following sections, we numerically explore the impact of larval competition d_l and released amount of *Wolbachia*-infected males p_w under two different levels of control targets: the high-level control target (that is, eradicating wild type mosquitoes) and the low-level control target (i.e., reducing mosquito population). Note that the population size of adult mosquitos, which can transmit the pathogen, is focused to study how larval competition and IIT jointly affect the population dynamics.

4.4. Population eradication vs. population reduction

In order to eradicate the wild type mosquito population, sufficiently large amount of *Wolbachia*-infected males should be continuously released. For high-level mosquito population eradication, the prerequisite condition is the capacity of sufficient production of *Wolbachia*-infected males. Under this precondition, the main concern is the required time for mosquito population eradication. Recall that Figure 3 indicates the basic offspring number will be



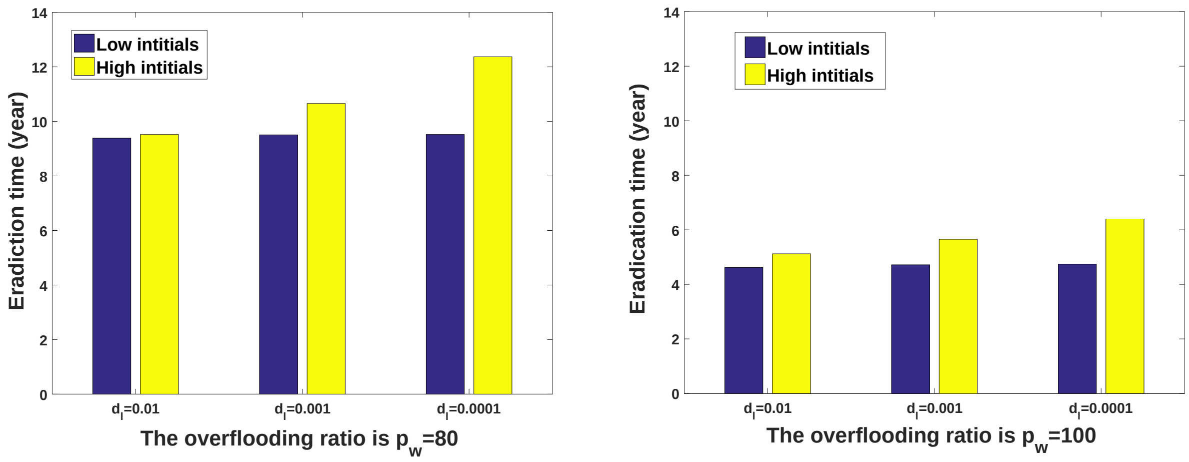
(a) $R_0 = 7.96, p_w = 10$



(b) $R_0 = 0.96, p_w = 80$

Figure 4: Threshold dynamics of immature and adult mosquito population in terms of the basic offspring number R_0 with different initial conditions. (a) R_0 takes the value of 7.96 when the overflooding ratio p_w is equal to 10. (b) $R_0 = 0.96 < 1$ when the overflooding ratio p_w takes the value of 80.

below 1 if the ratio of released *Wolbachia* infected males to wild type males is greater than 80. Here, we choose two cases of p_w, both of which are greater than 80. Then, we compare the required eradication time for these two cases. Figure 5 shows the variations of the required time to eradicate wild type mosquito population under various combinations of larval competition, the overflooding ratio and initial population sizes. The bar charts in Figure 5 indicate that eradication time declines with the increasing of larval competition and the overflooding ratio. However, the initial population size have the opposite effects on the eradication time. Thus, early release at the time of low mosquito abundance can substantially shorten the eradication time.



(a)

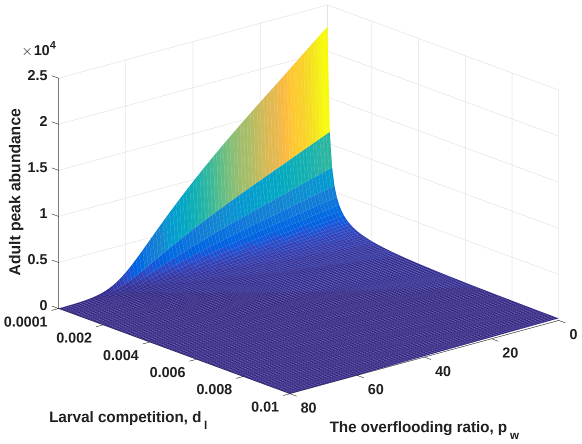
(b)

Figure 5: The time required for eradicating wild type mosquito population depends on the intensity of larval competition and initial population sizes when sufficiently large number of *Wolbachia*-infected males are released. (a) $p_w = 80$. (b) $p_w = 100$.

To achieve the goal of population eradication, sustained releases of large amount of *Wolbachia*-infected males are needed for at least 5 years, which will be a challenging task to achieve. Therefore, reducing the mosquito population size would be more realistic under limited production of *Wolbachia*-infected males. Our analytic results indicate that the mosquito population will approach to a globally stable periodic solution when $R_0 > 1$. Here, we use the peak value of the stable periodic solution for adult mosquitoes as the index to characterize the effectiveness of resulting population reduction. The integrated impacts of larval competition and IIT on suppression is explored in Figure 6(a). Mosquito reduction relies primarily on releasing *Wolbachia*-infected males since the peak adult abundance will drop down rapidly if the ratio of released *Wolbachia*-infected males to wild type males grows. In addition, the larval competition brings positive effects on reducing the adult peak abundance. Once the overflooding ratio is fixed, intensified larval competition will lower the ultimate peak adult abundance, regardless of the initial population size (see Figure 6(b)).

5. Discussion

The success of mosquito population suppression/eradication depends crucially on several factors including the biological features of the *Wolbachia* strain, the growth process of



(a)

(b)

Figure 6: (a) The variation of adult peak abundance with the overflooding ratio p_w and the larval competition d_l. (b) The dynamics of adult mosquito population under different levels of larval competition and initial mosquito population sizes. Here, the overflooding ratio is fixed as $p_w = 10$.

mosquitoes and the releasing strategies. The degree of larval competition is predicted to affect the survival probability of mosquitoes. Seasonal heterogeneities such as seasonal temperature variations are recognized to play important roles in regulating mosquito abundance, which will considerably affect the implement of IIT. To qualify the effectiveness of IIT, it is important to include these realistic aspects including seasonal environmental variations and density-dependent competition during larval stage. The classic McKendrick von-Foerster age-structured model was extended into a periodic partial differential equation with nonlinear density dependent death during the larval stage. Then, a new staged structured DDE model with periodic delays was derived, which incorporates the effects of larval competition not only in the death rate but also in the developmental rate of immature mosquitoes.

The stage structure model can be decoupled into only one equation for adults incorporating the effects of larval competition, which facilitates mathematical analysis and further model extension to the control of mosquito borne diseases. It should be noted that the model incorporates an additional death rate induced by intra-specific competition among larvae of the same age cohort. In reality, a mosquito larva may compete living resources with larvae from other age cohorts, which may trigger more complicated impacts on population dynamics, including larvae and adult survivorship, as well as the development time [56]. We expect this simple prototype model could serve as a starting point of modeling mosquito populations with more complicated consequences due to competition.

Under the assumption of continuous proportional releasing strategy, analytic analysis was conducted based on the decoupled model. By employing the method of next generation operator provided in [70], the basic offspring number R_0 was formulated, which serves as the threshold index to theoretically and numerically analyse the long term population dynamics. Threshold dynamics in terms of R_0 were established with the aid of theories of monotone dynamical system. These results indicate that the mosquito population will become extinction eventually when $R_0 < 1$ and approach to a stable periodic solution in the case of $R_0 > 1$.

Numerically, we simulated a hypothetical *Wolbachia*-free wild type mosquito population in Northern Australia. By employing the temperature data of Northern Australia, we fitted the time-periodic parameters. Based on these fitted parameters, the numerical results depicting the long-term dynamics of the solutions confirm our analytical results. Furthermore, compared with the corresponding time-periodic model, overestimates of R_0 are evident if seasonal factors are not considered.

In order to explore the integrated effects of larval competition and IIT, we consider two levels of mosquito control objectives, which are high-level population eradication and low-level population reduction respectively. Under high-level control objective, it is essential to know how long the release of *Wolbachia*-infected males will last to eradicate the mosquito population. Numerical results indicate that the required time for population eradication falls markedly with the increase of the overflooding ratio, stronger larval competition and smaller initial mosquito population size. For low-level control objectives, we use the peak abundance of the stable periodic solution to uncover the effectiveness of reduction. Similar to the case of high-level control objective, higher overflooding ratio and intensified larval competition play dominant roles in lowering the ultimate adult peak mosquito abundance. It is challenging to eradicate mosquito population with the IIT solely. It is imperative to integrate other traditional mosquito control approaches such as spraying larvicides to efficiently control mosquitoes.

Designing appropriate releasing strategies is the essential problem for IIT. Due to limited capacity of producing and sorting *Wolbachia*-infected males, continuous releasing can not be realized in most developing regions. Moreover, proportional release requires continuously monitoring the population size of natural wild type mosquitoes, which is another challenge to implement in the real situation. Frequently-used practical releasing strategies are discontinuous release such as impulsive and periodic release, which have been extensively modeled and analyzed in some wonderful studies without considering seasonal effects [20, 21, 23, 27, 28, 30]. Future work will consider more realistic discontinuous/impulsive release strategies, which leads to models with non-smooth or impulsive differential equations. It is also interesting to extend the population growth model to an epidemic model for disease control by combined utilisation of IIT and other intervention approaches.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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