

Complex behaviour in a dengue model with a seasonally varying vector population



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ABSTRACT

In recent decades, dengue fever and dengue haemorrhagic fever have become a substantial public health concern in many subtropical and tropical countries throughout the world. Many of these regions have strong seasonal patterns in rainfall and temperature which are directly linked to the transmission of dengue through the mosquito vector population. Our study focuses on the development and analysis of a strongly seasonally forced, multi-subclass dengue model. This model is a compartment-based system of first-order ordinary differential equations with seasonal forcing in the vector population and also includes host population demographics. Our analysis of this model focuses particularly on the existence of deterministic chaos in regions of the parameter space which potentially hinders application of the model to predict and understand future outbreaks. The numerically efficient 0–1 test for deterministic chaos suggested by Gottwald and Melbourne (2004) [18] is used to analyze the long-term behaviour of the model as an alternative to Lyapunov exponents. Various solutions types were found to exist within the studied parameter range. Most notable are the existence of isola n -cycle solutions before the onset of deterministic chaos. Analysis of the seasonal model with the 0–1 test revealed the existence of three disconnected regions in parameter space where deterministic chaos exists in the single subclass model. Knowledge of these regions and how they relate to the parameters of the model gives greater confidence in the predictive power of the seasonal model.

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1. Introduction

Dengue is a mosquito-borne virus that poses a growing world-wide threat [1]. The principle vector of dengue is the mosquito *Aedes aegypti*. The *A. aegypti* vector prefers artificial water containers such as pots, rain-water containers and discarded tyres for its breeding sites. Hatching typically occurs during wet periods, most likely after periods of rainfall when breeding sites are most suitable [2]. The sensitivity of *A. aegypti* populations, and hence the transmission of dengue, to ecological factors such as temperature and rainfall is well documented [3,4]. In many tropical countries, the seasonal variations of rainfall and temperature gives rise to seasonal patterns in the reported outbreaks of dengue fever [5]. This effect is particularly noticeable in regions that have distinct wet seasons such as North Queensland, Australia [6], Puerto Rico [7] and Thailand [5].

In the recent decade, a variety of mathematical models have been developed to study the irregular seasonal patterns in dengue epidemics that occur throughout the world (for example, [8–14]). This paper investigates a multiple subclass seasonal dengue model,

motivated by Chowell et al. [15]. Our model differs from many seasonal models by including the dynamics of the vector population, incorporating seasonal forcing through a periodic variation as in Bacaër et al. [16], and through the use of multiple subclasses to replicate the dynamics of dengue incubation and infectious periods. As demonstrated by Kuznetsov et al. [17], the inclusion of seasonal forcing in an Susceptible, Infective, Recovered (SIR) type compartment model gives rise to parameter regions within which deterministic chaos is possible. For the purpose of using a model to predict and understand disease transmission, the existence of deterministic chaos in the model makes the application of the model within certain parameter regions less useful. Regardless of the limitations imposed by deterministic chaos, seasonally forced models are essential should any forecast be desired in regions where there is a strong seasonal nature to the mosquito population.

Of interest here is the long-term dynamics of the model and the type of behaviour that is possible. We use bifurcation analysis to study solution dynamics under parameter variations. Our bifurcation analysis quantifies the long-term solution dynamics within the parameter space into steady-state solutions, periodic solutions and non-periodic solutions. For non-periodic solutions, the solution type is classified through the application of the numerically efficient 0–1 test for deterministic chaos [18,19]. The 0–1 test is an alternative method to using Lyapunov exponents and produces

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a binary output for a given time series data without the need for QR decomposition. This output is either near 1 which indicates the presence of deterministic chaos or near 0 otherwise. We investigate the regions of parameter space within which deterministic chaos exists for our model in addition to the various long-term solution dynamics that arise. Ascertaining where in parameter space chaotic solutions are present and quantifying the types of complex behaviour that is possible allows for the confident use of our model when investigating possible future dengue outbreaks. This paper lays the groundwork for future studies that extend this model by the inclusion of multiple strains and an explicit dependence of the vector population on ecological factors such as temperature and rainfall.

2. A seasonal dengue model

The sensitivity of mosquito populations and the transmission of mosquito-borne pathogens to both temperature and hydrologic variability is a well established fact [3]. Various independent studies have confirmed the *A. aegypti* population dependence with respect to rainfall [20] and temperature [4,21]. Many tropical regions in the world experience marked variation in temperature and rainfall with distinct wet and dry seasons. For example, far North Queensland, Australia experiences heavy rainfall during summer months and almost negligible rainfall during winter months [22] as is evident in Fig. 1. Similar patterns in climate seasonality with noticeable wet seasons are encountered in regions such as Puerto Rico [7], Indonesia [23] and Thailand [5]. This strong seasonality has a dramatic impact on the mosquito population in these climate zones and hence a seasonal forcing is required to properly implement the climate dependent population dynamics of the *A. aegypti* vector. Our mathematical model in this paper advances upon the work previously undertaken by [15] by including demographics in the host population and introducing a seasonal forcing to the female *A. aegypti* population. The aim here is to provide a model that has similar dynamics to the dengue outbreak data encountered within regions such as Queensland, Australia (Population: 4,659,000 as of June 2013) as shown in Fig. 2. The Queensland data generally has small seasonal peaks with

occasional large peaks. Outbreaks are not endemic and recede each year during the dry season.

To represent the known characteristics of dengue incubation and infective periods in both human host and mosquito vector, a multi-subclass model will be used. Following directly from [15], this model introduces e_h incubation subclasses in the exposed host population ($E_{h_1}, E_{h_2}, \dots, E_{h_{e_h}}$), e_v subclasses in the exposed vector population ($E_{v_1}, E_{v_2}, \dots, E_{v_{e_v}}$) and i_h infectious subclasses in the host population ($I_{h_1}, I_{h_2}, \dots, I_{h_{i_h}}$). The rates of progression between the subclasses are given by $e_h k_h$ and $e_v k_v$ for the incubation periods of the human and mosquito population, respectively and $i_h \gamma_h$ for the infectious period in humans. Using multiple subclasses results in the infectious and incubation periods being gamma distributed [25,26] with means $1/k_v, 1/k_h$ and $1/\gamma_h$ for the incubation and infectious periods, respectively and the corresponding variances of the gamma distributions are given by $1/(e_v k_v^2), 1/(e_h k_h^2)$ and $1/(i_h \gamma_h^2)$, respectively. Our multi-subclass dengue model with seasonality and demographics is given by the following system of $(4 + e_h + e_v + i_h)$ first-order differential equations for the population in each compartment:

$$\begin{aligned} \dot{S}_h(t) &= \mu_h N_h(t) - (\mu_h + \lambda_v(t)) S_h(t), \\ \dot{E}_{h_1}(t) &= \lambda_v(t) S_h(t) - (k_h e_h + \mu_h) E_{h_1}(t), \\ \dot{E}_{h_j}(t) &= k_h e_h E_{h_{j-1}}(t) - (k_h e_h + \mu_h) E_{h_j}(t), \quad 2 \leq j \leq e_h, \\ \dot{I}_{h_1}(t) &= k_h e_h E_{h_{e_h}}(t) - (\gamma_h i_h + \mu_h) I_{h_1}(t), \\ \dot{I}_{h_j}(t) &= \gamma_h i_h I_{h_{j-1}}(t) - (\gamma_h i_h + \mu_h) I_{h_j}(t), \quad 2 \leq j \leq i_h, \\ \dot{R}_h(t) &= \gamma_h i_h I_{h_{i_h}}(t) - \mu_h R_h(t), \\ \dot{S}_v(t) &= \mu_v n_v(t) - (\mu_v + \lambda_h(t)) S_v(t), \\ \dot{E}_{v_1}(t) &= \lambda_h(t) S_v(t) - (k_v e_v + \mu_v) E_{v_1}(t), \\ \dot{E}_{v_j}(t) &= k_v e_v E_{v_{j-1}}(t) - (k_v e_v + \mu_v) E_{v_j}(t), \quad 2 \leq j \leq e_v, \\ \dot{I}_v(t) &= k_v e_v E_{v_{e_v}}(t) - \mu_v I_v(t), \end{aligned} \tag{1}$$

where $\lambda_h(t) = C\beta_{vh} \frac{\sum_{j=1}^{e_h} I_{h_j}(t)}{N_h(t)}$ and $\lambda_v(t) = C\beta_{hv} \frac{I_v(t)}{N_h(t)}$. The total human population is given by $N_h(t) = S_h(t) + \sum_{j=1}^{e_h} E_{h_j}(t) + \sum_{j=1}^{i_h} I_{h_j}(t) + R_h(t)$

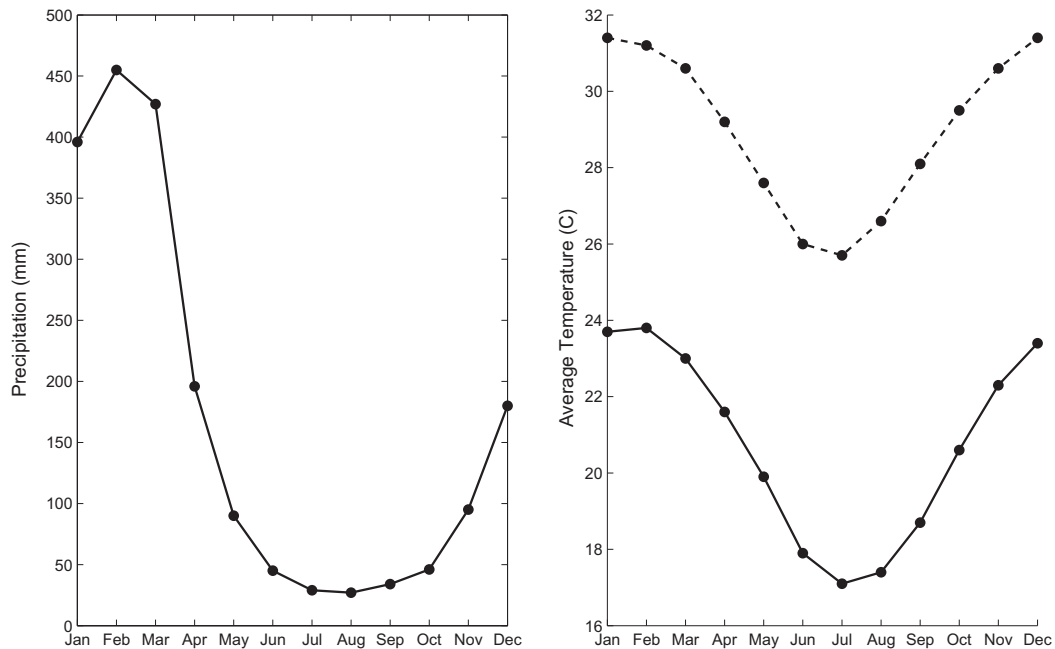


Fig. 1. Climate data for Cairns Aero AWS, North Queensland retrieved from [22]. Left: average monthly rainfall. Right: average monthly high and low temperatures.

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