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Effects of seasonal variation patterns on recurrent outbreaks in epidemic models

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HIGHLIGHTS

- We propose a method to analyze epidemic models with piecewise constant seasonality.
- Square wave forcing has a higher effective seasonal intensity than sinusoidal forcing.
- The temporal variation pattern of seasonality influences recurrent outbreak patterns.
- A realistic seasonal variation pattern can be successfully analyzed by our method.
- Accurate estimations of seasonality from data would be important.

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ABSTRACT

Transmission of infectious diseases often depends on seasonal variability. Mathematical epidemic models driven by seasonal forcing have been widely explored to understand recurrent outbreaks of infectious diseases. Here we present an effective method to examine the impact of seasonal variation patterns on epidemic dynamics. The idea is to represent the seasonal variability as a piecewise constant function and analyze the seasonally forced epidemic model by means of a numerical shooting method for switched dynamical systems. Several illustrative examples demonstrate that our method is useful to elucidate the effects of various types of seasonality in outbreak behavior. First, we clarify an effect of the shape of seasonal forcing by comparing sinusoidal and square wave forcing functions. Second, we demonstrate that not only the intensity of seasonality but also its temporal variation pattern significantly influences the outbreak pattern. Finally, we reveal the mechanisms of transitions between different outbreak patterns in an epidemic model driven by realistic term-time seasonal forcing and one driven by seasonal forcing estimated from real data. Our results suggest that accurately estimated seasonal variability is necessary for better understanding the dynamics of infectious diseases.

1. Introduction

Seasonality is very common in ecological and social systems. In a macroscopic viewpoint, almost similar variation patterns in climate and human social behavior are repeated every year, although there may be minor long-term changes (Soper, 1929). A number of reported cases have suggested that seasonality plays an important role in epidemic outbreaks (Fine and Clarkson, 1982; Finkenstädt and Grenfell, 2000; Dowell, 2001). For instance, seasonal influenza epidemics occur yearly during winter in temperate regions (Truscott et al., 2012). In warmer regions, the timings of outbreaks of meningococcal and measles epidemics coincide with the beginning of the dry season in each year (Greenwood et al., 1984; Ferrari, 2008). The major factors of seasonality related to human infectious diseases can be categorized into several different types (Dowell, 2001; Grassly and Fraser, 2006; Altizer et al., 2006; Fisman, 2007) such as survival of pathogens in the environment, host behavior, host immune function, and abundance of vectors and non-human hosts. For infectious diseases of wildlife, seasonal reproduction can also be influential in addition to the above factors (Altizer et al., 2006). However, the biologically distinct mechanisms of seasonality are not independent of each other, because most of them more or less depend on the annual variation in the environment such as temperature, humidity, rainfall, sunlight, and wind. It is still challenging to understand the mechanisms of seasonality and their impacts on the dynamics of infectious diseases.

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Mathematical modeling is a common and effective approach to investigate how seasonality influences epidemic outbreaks (Anderson and May, 1991). Population-based epidemic models driven by seasonal forcing have been explored to account for recurrent outbreaks of infectious diseases, particularly for multi-annual outbreak cycles in childhood diseases. Seasonality has often been incorporated into the population models by representing the transmission rate as a sinusoidal forcing function. Sinusoidally forced SIR (susceptible-infectious-recovered) type models are capable of reproducing biennial outbreaks as observed in measles epidemics during the pre-vaccination era as well as multi-annual cycles and erratic patterns as observed in other childhood diseases such as chickenpox, mumps, pertussis, and rubella (London and Yorke, 1973; Dietz, 1976). The annual and multi-annual cycles correspond to harmonic and subharmonic solutions of the mathematical models, respectively, which are typically found in periodically forced nonlinear dynamical systems (Schwartz and Smith, 1983; Smith, 1983; Aron and Schwartz, 1984). Chaotic dynamics in the deterministic models gives a possible explanation for irregular outbreaks in childhood diseases, as supported by time series analysis of incidence data (Schaffer, 1985; Schaffer and Kot, 1985; Olsen and Schaffer, 1990; Mollison and Din, 1993; Tidd et al., 1993; Bolker and Grenfell, 1993; Rohani et al., 1998). Qualitative changes in the outbreak pattern with a variation of one or more system parameters can be examined by a phase diagram (or a bifurcation diagram) in which the period of the outbreak cycle is indicated to changes of parameter values (Truscott et al., 2012; Ferrari, 2008; Bolker and Grenfell, 1993; Rand and Wilson, 1991; Kuznetsov and Piccardi, 1994; Lloyd, 2001; Kamo and Sasaki, 2002; Greenman et al., 2004; Casagrandi et al., 2006; Childs and Boots, 2010). A numerical bifurcation analysis enables to identify boundaries between parameter regions of different outbreak cycles and clarify the impact of a seasonality parameter on epidemic dynamics (Kuznetsov and Piccardi, 1994; Lloyd, 2001; Casagrandi et al., 2006). However, this analysis method is directly applicable only to smooth dynamical system models with a continuous seasonal forcing function such as the sinusoidal one.

Instead of the sinusoidal function which is a poor representation of the actual pattern of seasonality, discontinuous seasonal forcing functions have also been widely taken into consideration. The square wave forcing has been used under the assumption that each year is simply divided into two seasons with high and low transmission rates (Stone et al., 2007). The term-time forcing has been introduced to examine spreading of childhood diseases in schools, which sets the transmission rate at a high level during school terms and at a low level during holidays (Schenzle, 1984). The seasonality that can be estimated from real infection data corresponds to the term-time forcing rather than the sinusoidal forcing (Fine and Clarkson, 1982; Finkenstädt and Grenfell, 2000). Therefore, the term-time forcing based on the actual schedule of schools in England and Wales has been employed in many studies (Earn et al., 2000; Keeling et al., 2001; Bauch and Earn, 2003; Britton and Lindholm, 2009; Black and McKane, 2010). Furthermore, a recent study revealed that the seasonality of the estimated transmission rate varies depending on the type of childhood disease (Metcalf et al., 2009).

In order to deal with discontinuous seasonal variability, we introduce a numerical shooting method to analyze bifurcations in SIR-type epidemic models driven by a piecewise constant forcing function which is capable of approximating any seasonal variation pattern. In Section 2, we describe the conditional equations to specify periodic outbreaks and their transitions by using a Poincaré map constructed as a composite of multiple submaps. In Section 3, we illustrate that our method is useful to elucidate the impact of various seasonal variation patterns on recurrent outbreaks through several illustrative examples. First, we focus on the square wave and sinusoidal forcing functions to study how the shape of the seasonal forcing function influences the outbreak behavior. Although both forcing functions cause irregular outbreak patterns when the intensity of the seasonality is high, the difference between them is not well understood (Altizer et al., 2006). Thus, we compare the two forcing functions by constructing detailed phase diagrams in the space of seasonality parameters. Second, we investigate the effects of temporal variation patterns of seasonality on the outbreak behavior. The seasonal forcing is assumed to be a piecewise constant function including two seasons with high and low transmission rates. We show that the ratio between the durations of the two seasons considerably affects the outbreak pattern when the baseline of the transmission rate is fixed. Our results indicate that the outbreak pattern depends on the intensity of the seasonality as well as its temporal variation pattern. Finally, we show that our method is applicable to analyses of an epidemic model with a realistic term-time forcing (Keeling et al., 2001) and one with a seasonal transmission rate estimated from reported cases (Metcalf et al., 2009). Our method clarifies the mechanisms of transitions in the outbreak pattern and detects parameter regions for coexisting multiple outbreak patterns. In Section 4, we discuss possibilities of making use of our analysis method for better understanding infectious disease dynamics.

2. Methods

SIR-type epidemic models driven by a piecewise constant forcing function are regarded as switched dynamical systems. In this section, we introduce a shooting method to locate a periodic solution and its bifurcation sets in switched dynamical systems (Kousaka et al., 1999; Tsumoto et al., 2006; Tanaka et al., 2008). By using this numerical method, we can make a phase diagram with boundary curves separating different outbreak regimes and thereby reveal the effects of seasonality parameters as demonstrated in the next section.

2.1. A model driven by a periodic piecewise constant forcing function

We consider an epidemic model represented by the following form:

$$\dot{\mathbf{x}}(t) = \mathbf{f}(\mathbf{x}(t),\lambda(t)), \tag{1}$$

where $\mathbf{x}(t) \in R^n$ denotes the state vector at time $t \in R$, $\mathbf{f}$ represents a C^∞-class mapping for all state variables and parameters, and $\lambda(t) \in R$ is a time-varying parameter representing seasonality. For a standard SIR model, $\mathbf{x}(t) = (S(t),I(t),R(t))^T$ where S, I, and R represent the populations of susceptible, infectious, and recovered individuals, respectively. We assume that the seasonal forcing $\lambda(t)$ is periodic with period T which normally corresponds to one year. We assume that the nth term from $t=nT$ to $t=(n+1)T$ $(n=0,1,\ldots)$ is described by the piecewise constant function with k intervals as follows:

$$\lambda(nT+t') = \begin{cases} \lambda_0 & (\tau_0 = 0 \le t' < \tau_1), \\ \vdots & \vdots \\ \lambda_i & (\tau_i \le t' < \tau_{i+1}), \\ \vdots & \vdots \\ \lambda_{k-1} & (\tau_{k-1} \le t' < \tau_k = T), \end{cases} \tag{2}$$

where λ_i $(i=0,\ldots,k-1)$ is constant. The duration of the ith interval is given by $\Delta\tau_i \equiv \tau_{i+1}-\tau_i$. The flow of the system in the ith interval is denoted by $\varphi_i(s,\mathbf{x}(nT+\tau_i))$ where $s \equiv t'-\tau_i$. We assume that the orbit is continuous at the time $t'=\tau_i$ $(i=0,\ldots,k-1)$ when the parameter λ is switched.