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Tong Li

Yi Li, *Wright State University - Main Campus*

Herbert W. Hethcote



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Periodic Traveling Waves in SIRS Endemic Models

Tong Li

Yi Li

Department of Mathematics

Department of Mathematics

University of Iowa

University of Iowa

14 MacLean Hall

14 MacLean Hall

Iowa City, IA 52242, USA

Iowa City, IA 52242, USA

Corresponding author

yli@math.uiowa.edu

email: tli@math.uiowa.edu

phone: 319-335-3342

FAX: 319-335-0627

Herbert W. Hethcote
Department of Mathematics
University of Iowa
14 MacLean Hall
Iowa City, IA 52242, USA
herbert-hethcote@uiowa.edu

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Abstract

Mathematical models are used to determine if infection wave fronts could occur by traveling geographically in a loop around a region or continent. These infection wave fronts arise by Hopf bifurcation for some spatial models for infectious disease transmission with distributed-contacts. Periodic traveling waves are shown to exist for the spatial analog of the SIRS endemic model in which the temporary immunity is described by a delay, but they do not exist in a similar spatial SIRS endemic model without a delay. Specifically, we found that the ratio of the delay ω in the recovered class and the average infectious period $1/\gamma$ must be sufficiently large for Hopf bifurcation to occur.

Keywords: periodic, traveling waves, infectious diseases, models, differential equations, delay-differential equations, Hopf bifurcation

1 Introduction

Infectious diseases spread geographically as shown on maps with isodate spread contours [2, 9, 37, 43]. Some estimated speeds of spatial propagation are about 140 miles per year for the plague in Europe in 1347-1350 [43], 30-60 kilometers per year for fox rabies in Europe starting in 1939 [43], 18-24 miles per year for raccoon rabies in the Eastern United States starting in 1977 [7], and worldwide spread in one year for influenza in the 20th century [51].

Here we use mathematical modeling to investigate the question of whether an animal or human disease could persist as a wave front of infectives that travels geographically around a large loop; for example, it could go from country to country around a continent. Thus we visualize that by the time a disease returns to one border of a country, there are enough new susceptibles in that country, so that the disease wave front could travel across that country to another border and then continue across the next country in the loop. We find that these periodic traveling infection wave fronts cannot occur in an SIRS endemic model with exponential waiting times in both the I and R compartments, but they can occur in an SIRS endemic model in which the temporary immunity is described by a long enough delay.

The book by Murray [43] contains many examples of traveling wave solutions and a chapter on the spatial spread of epidemics. Other books also have sections of spatial epidemic spread and traveling waves [6, 10, 16, 46]. There are also many models for the geographic spread of specific diseases [8, 14, 50, 55]. Spatial heterogeneity has been described by epidemiology models with spatial patch

structures [6, 19, 25]. Epidemic spread has also been studied using lattice and cellular automata models [15, 48, 49].

Traveling wave solutions and wavetrain solutions for general reaction diffusion systems with limit cycle kinetics were studied by Kopell and Howard in their seminal papers [30] and [31], where the authors attempted to describe the formation of colour patterns in the Zhabotinski-Belousov reaction and to prove the existence of homogeneous target pattern and spiral solutions to " λ - ω " systems. For example in [30], the authors considered $\frac{\partial x}{\partial t} = F(x) + k\Delta x$ where x is the concentration of the chemical reactants, and investigated the plane-wave solutions, which are of the form $x(z, t) = y(\sigma t - \alpha \cdot z)$, where y is a 2π -periodic function, $\sigma > 0$ is the angular frequency and α the wave-number vector of the plane wave. The existence and stability of such solutions were discussed. It was shown that low-amplitude waves are always unstable and that the stability of the higher-amplitude waves depends on the nature of the nonlinearity of the chemical-reaction equations. Since then there have been many studies at periodic traveling waves, see [4, 12, 32, 40, 45, 52] and references therein. For example in [32], Kot examined the varied traveling waves that arise in some simple ecologically-interesting integrodifference equations. In particular for a scalar equation with compensatory growth, the author observed only simple traveling waves. A model with overcompensation exhibited flip bifurcations and traveling cycles in addition to simple traveling waves. Finally, the author also observed that a simple predator-prey system possessed periodic wave trains and a variety of traveling waves.

2 Formulation of Non-spatial Endemic Models

Epidemic models are used to describe rapid outbreaks that occur in less than one year, while endemic models are used for studying diseases over longer periods, during which there is a renewal of susceptibles by births or recovery from temporary immunity. We consider endemic models in which people move cyclically among compartments corresponding to three epidemiological states. Those who can be infected are in the susceptible compartment S . When there is an adequate contact of a susceptible with an infective so that transmission occurs, then the susceptible enters the compartment I of infectives, who are infectious in the sense that they are capable of transmitting the infection. When the infectious period ends, the individual enters the recovered compartment R . When the infection-acquired immunity wanes, the individual move back to the susceptible class. Based on the order of flow through the epidemiological compartments, this model is called an SIRS model.

The incidence is the infection rate of susceptible individuals through their contacts with infectives. If $S(t)$ is the number of susceptibles at time t , $I(t)$ is the number of infectives, and N is the total population size, then $s(t) = S(t)/N$ and $i(t) = I(t)/N$ are the susceptible and infectious fractions, respectively. If β is the average number of adequate contacts (*i.e.* contacts sufficient for transmission) of a person per unit time, then $\beta I/N = \beta i$ is the average number of contacts with infectives per unit time of one susceptible, and $(\beta I/N)S = \beta N i s$ is the number of new cases per unit time at time t due to the $S = N s$ susceptibles. This form of the incidence is called the standard incidence, because

it is formulated from the basic principles above [19, 20, 21]. This form is also called the frequency-dependent incidence, because it depends on the frequency of infection I/N [5, 27].

A common assumption is that the movement out of the I compartment is governed by γI , which corresponds to an exponentially distributed waiting time in the I compartment. Similarly, the movement out of the R compartment back to the S compartment in an SIRS model described by δR corresponds to an exponential waiting time in R . For an SIRS model with exponential waiting times in both the I and R compartments, it has been shown that when the disease remains endemic, all solutions approach the endemic equilibrium. Therefore there are no periodic solutions [19].

Another possible assumption is that the fraction still in the compartment t units after entering is a non-increasing, piecewise continuous function $P(t)$ with $P(0) = 1$ and $P(\infty) = 0$. Then the rate of leaving the compartment at time t is $-P'(t)$ so the mean waiting time in a compartment is $E[a] = \int_0^\infty t(-P'(t))dt = \int_0^\infty P(t)dt$. These distributed delays lead to epidemiology models in the form of integral or integro-differential or functional differential equations. If the waiting time distribution is a step function given by $P(t) = 1$ if $0 \leq t \leq \omega$, and $P(t) = 0$ if $\omega < t$, then the mean waiting time is ω and the model reduces to a delay-differential equation for $t \geq \omega$ [24]. For an SIRS model with a constant temporary immunity time ω , it has been shown that periodic solutions arise by Hopf bifurcation when the ratio of the temporary immunity time ω to the average infectious period $\frac{1}{\gamma}$ is sufficiently large [23]. We investigate a spatial

analog of this SIRS model in this paper.

The basic reproduction number R_0 is defined as the average number of secondary infections that occur when one infective is introduced into a completely susceptible host population [11]. It is implicitly assumed that the infected outsider is in the host population for the entire infectious period and mixes with the host population in exactly the same way that a population native would mix. The contact number σ is defined as the average number of adequate contacts of a typical infective during the infectious period [19, 25]. An adequate contact is one that is sufficient for transmission, if the individual contacted by the susceptible is an infective. For the models considered here, the contact number σ remains constant as the infection spreads, so it is equal to the basic reproduction number R_0 [21].

3 A Simple Spatial SIRS Model

For many types of spatial epidemiology models in infinite domains, one often determines the thresholds above which a traveling wave exists, finds the minimum speed of propagation and the asymptotic speed of propagation (which is usually shown to be equal to the minimum speed), and determines the stability of the traveling wave to perturbations [33, 39, 41, 43, 46, 54]. For spatial models in finite domains, stationary states and their stability have been investigated [6]. For stochastic spatial endemic models there is also a threshold condition, so that the disease dies out below the threshold and approaches an endemic

stationary distribution above the threshold [13].

There are several possible ways to formulate spatial epidemiology models [41, 47, 55]. Distributed contact models are formulated by using integral equations with kernels describing daily contacts of infectives with their neighbors [29, 42]. Diffusion-based epidemiology models are formulated from non-spatial models by adding diffusion terms corresponding to the random movements each day of susceptibles and infectives [38, 44]. Reluga, Medlock and Galvani [47] formulated a restricted-movement model in which each individual has a home position about which the individual moves in a biased random walk. They assumed that the probability distribution of an individual's position approaches a stationary Gaussian distribution for large time. In the limit when the homeward attraction is much larger than the transmission rate, their model approximates a distributed-contacts model. When the transmission rate is much larger than the homeward attraction and diffusion is much faster than homeward attraction, their model is approximately a diffusive distributed-infectives model. When the transmission rate is much larger than the homeward attraction and diffusion effects are weak, their model is approximately an advective distributed-infectives model [47].

In order to investigate the existence of infection waves that travel geographically around a continent or country, we consider a distributed-contacts spatial analog of the basic SIRS endemic model in one space dimension. Assume that the density of the population is constant on $(-\infty, \infty)$. Let $s(t, x)$ and $i(t, x)$ be the relative densities (i.e. fractions of the population density at position x) of

the susceptibles and infectives at time t and position x . The kernel $K(x, y)$ is analogous to the contact rate β , so it is the number of adequate contacts of an infective at position y with a susceptible at position x . Thus the distributed-contacts spatial analog of the basic SIRS endemic model [21] is given by the initial value problem

$$\begin{aligned} \partial s / \partial t &= - \int_{-\infty}^{\infty} K(x, y) i(t, y) dy s(t, x) + \delta r(t, x), & s(0, x) = s_0(x) \geq 0, \\ \partial i / \partial t &= \int_{-\infty}^{\infty} K(x, y) i(t, y) dy s(t, x) - \gamma i(t, x), & i(0, x) = i_0(x) \geq 0, \\ \partial r / \partial t &= \gamma i(t, x) - \delta r(t, x), & r(0, x) = r_0(x) \geq 0 \end{aligned} \tag{3.1}$$

where $\delta > 0$, $\gamma > 0$. $1/\delta$ is the average period of temporary immunity and $1/\gamma$ the average infectious period. Moreover, $s(t, x) + i(t, x) + r(t, x) = 1$ because the relative densities add up to one. Since there is an inflow into the susceptible class from the recovered class in this SIRS model, vital dynamics (births and deaths) are not included. We assume that the kernel and the initial conditions are smooth, so that unique solutions of (3.1) exist and remain nonnegative for all positive time [18].

We now derive a diffusion approximation to the system (3.1) following the approaches used by Bailey [3] and Hoppensteadt [28]. Assume that the distribution of adequate contacts depends only on the distance from position y to position x , so the kernel is given by $K(x, y) = k(x - y)$. Assume that the kernel is continuous and symmetric with $k(-y) = k(y)$, and that contacts are local, so that $k(y) = 0$ for $y \geq \varepsilon$, where ε is some small number. Also assume that the function $i(t, y)$ does not change very much over the set of radius ε ; here we

assume that the 4th derivatives of i with respect to y are $O(1)$ on such a set.

By changing variables in the integral, we obtain

$$\int_{-\infty}^{\infty} k(x-y)i(t,y)dy = \int_{-\infty}^{\infty} k(z)i(t,x-z)dz.$$

Note that $i(t, x-z)$ can be expanded using Taylor's formula to obtain

$$i(t, x-z) = i(t, x) - z \frac{\partial i(t, x)}{\partial x} + \frac{1}{2} z^2 \frac{\partial^2 i(t, x)}{\partial x^2} - \frac{1}{6} z^3 \frac{\partial^3 i(t, x)}{\partial x^3} + \frac{1}{24} z^4 \frac{\partial^4 i(t, x^*)}{\partial x^4}$$

where x^* is some point between x and $x-z$. Substituting this expansion into

the second integral above leads to

$$\begin{aligned} \int_{-\infty}^{\infty} k(x-y)i(t,y)dy &= \int_{-\infty}^{\infty} k(z)dz i(t, x) - \int_{-\infty}^{\infty} k(z)zdz \frac{\partial i(t, x)}{\partial x} \\ &+ \int_{-\infty}^{\infty} \frac{1}{2} k(z)z^2 dz \frac{\partial^2 i(t, x)}{\partial x^2} - \int_{-\infty}^{\infty} \frac{1}{6} k(z)z^3 dz \frac{\partial^3 i(t, x)}{\partial x^3} + \int_{-\infty}^{\infty} \frac{1}{24} k(z)z^4 \frac{\partial^4 i(t, x^*)}{\partial x^4} dz. \end{aligned}$$

Because the kernel is symmetric with $k(-y) = k(y)$, the integrals in the second and the fourth terms on the right hand side vanish. Since the fourth derivatives of i with respect to y are $O(1)$, the fifth term on the right hand side is $O(\varepsilon^4)$, so it is neglected. Letting the integral in the first term be β and the integral in the third term be D , we have the diffusion approximation

$$\int_{-\infty}^{\infty} k(x-y)i(t,y)dy \approx \beta i(t, x) + D i_{xx}(t, x), \quad (3.2)$$

Using $s(t, x) = 1 - i(t, x) - r(t, x)$, the diffusion approximation of the system (3.1) becomes

$$\begin{aligned} \partial i / \partial t &= (\beta i + D i_{xx}) (1 - i - r) - \gamma i, & i(0, x) &= i_0(x) \geq 0, \\ \partial r / \partial t &= \gamma i - \delta r, & r(0, x) &= r_0(x) \geq 0. \end{aligned} \quad (3.3)$$

We are looking for traveling wave solutions, so we assume that $i(t, x) = f(x + ct) = f(\xi)$ and $r(t, x) = g(x + ct) = g(\xi)$ with $\xi = x + ct$ and c is the traveling wave speed. Let $f' = u$, so that $u' = f''$, which leads to the three dimensional system

$$\begin{aligned} f' &= u, \\ u' &= \frac{cu + \gamma f}{D(1 - f - g)} - \frac{\beta f}{D}, \\ g' &= \frac{\gamma}{c}f - \frac{\delta}{c}g. \end{aligned} \tag{3.4}$$

The equilibrium points of this system are the disease-free equilibrium at the origin and the endemic equilibrium

$$\begin{pmatrix} f \\ u \\ g \end{pmatrix} = \begin{pmatrix} \frac{1-1/\sigma}{1+q} \\ 0 \\ q \frac{1-1/\sigma}{1+q} \end{pmatrix}, \tag{3.5}$$

where $\sigma = \beta/\gamma$ is the contact number and $q = \gamma/\delta = (1/\delta)/(1/\gamma)$ is the quotient of the average period $1/\delta$ of temporary immunity and the average infectious period $1/\gamma$. If $\sigma > 1$, then the endemic equilibrium is in the epidemiologically realistic region where $f > 0$ and $g > 0$.

The linearization of (3.4) at the origin has a characteristic equation $(\lambda + \delta/c)[D\lambda^2 - c\lambda + \gamma(\sigma - 1)] = 0$, so that one root is $-\delta/c$ corresponding to a one-dimensional stable manifold in the g direction. The other two roots are

$$\lambda_{1,2} = \frac{c \pm \sqrt{c^2 - 4\gamma D(\sigma - 1)}}{2D}. \tag{3.6}$$

When $\sigma > 1$ and $c \geq c_{\min} = 2\sqrt{D\gamma(\sigma - 1)}$, both eigenvalues are positive real numbers, so that the origin has a two-dimensional unstable manifold. Thus for

$c \geq c_{\min}$, there is a repulsive direction away from the origin. The usual phase plane approach [43] is to show that the endemic equilibrium has an attractive direction in the region in which $u > 0$ and f is less than the endemic value, so that a heteroclinic orbit joining the origin and the endemic equilibrium would correspond to a traveling wave solution. This geometric argument does not work in three space dimensions, but here we are interested in periodic traveling wave solutions, which correspond to periodic solutions in the phase plane.

The Hopf bifurcation theorem states that under certain conditions a branch of periodic solutions splits off from an equilibrium when the real part of a complex conjugate pair of eigenvalues changes sign as the parameters change [17, pp.150-56]. The system of differential equations $\dot{\mathbf{x}} = \mathbf{h}(\mathbf{x}, \mu)$ with $\mathbf{x} \in R^n$, $\mu \in R$, smooth \mathbf{h} , and an equilibrium point given by $\mathbf{x} = \mathbf{x}_0(\mu)$ is said to have a Hopf bifurcation at $\mu = \mu_0$ if the equilibrium \mathbf{x}_0 bifurcates into a "small amplitude" periodic solution as μ passes through μ_0 . The conditions for a Hopf bifurcation are 1) the Jacobian $\mathbf{J}(\mu) = \mathbf{D}_{\mathbf{x}}\mathbf{h}(\mathbf{x}_0(\mu), \mu)$ has a pair of complex conjugate eigenvalues $\alpha(\mu) \pm i\beta(\mu)$, 2) for some value $\mu = \mu_0$, $\alpha(\mu_0) = 0$, $\beta(\mu_0) > 0$, $\alpha'(\mu_0) \neq 0$ so that the sign of the real part $\alpha(\mu)$ changes which is called the transversality condition; and 3) the remaining eigenvalues of $\mathbf{J}(\mu_0)$ have nonzero real parts. In order for Hopf bifurcation to occur, the characteristic equation at the equilibrium point must have pure imaginary roots for some parameter values.

If there is a periodic solution with $f(\xi + P) = f(\xi)$ and $g(x + P) = g(\xi)$, around the endemic equilibrium in the region with $f > 0$ and $g > 0$ for some

$P > 0$, then it corresponds to a periodic traveling wave solution. We now show that periodic solutions do not arise around the endemic equilibrium by Hopf bifurcation. The Jacobian at the endemic equilibrium (3.5) is

$$\mathbf{J} = \begin{bmatrix} 0 & 1 & 0 \\ A & \frac{\sigma c}{D} & A \\ \frac{\gamma}{c} & 0 & -\frac{\delta}{c} \end{bmatrix},$$

where $A = [\gamma\sigma(\sigma - 1)]/[D(1 + q)] > 0$. This leads to the characteristic equation

$$-\lambda^3 + \left(\frac{\sigma c}{D} - \frac{\delta}{c}\right)\lambda^2 + \left(A + \frac{\sigma\delta}{D}\right)\lambda + \frac{\gamma A}{c}\left(1 + \frac{1}{q}\right) = 0.$$

After substituting $\lambda = i\mu$, the real and imaginary parts become

$$\left(\frac{\sigma c}{D} - \frac{\delta}{c}\right)\mu^2 - \frac{\gamma A}{c}\left(1 + \frac{1}{q}\right) = 0 \text{ and } \mu(\mu^2 + A + \frac{\sigma\delta}{D}) = 0.$$

Since $A + \frac{\sigma\delta}{D} > 0$, the second equation has no non-zero real roots, so that there are no pure imaginary roots. Thus Hopf bifurcation cannot occur, so that periodic traveling wave solutions of the model (3.3) do not arise by Hopf bifurcation.

4 A Spatial SIRS Model with a Delay in R

The non-spatial SIRS model with a delay in the removed class has a periodic solution if the delay is sufficiently large [23]. Here we show that the spatial analog also has a periodic traveling wave solution if the delay is sufficiently large. Let the waiting time distribution in the removed class R be a step function given by $P(t) = 1$ if $0 \leq t \leq \omega$, and $P(t) = 0$ if $\omega < t$. Then the distributions of

epidemiological classes for this SIRS model with $t \geq 0$ satisfy

$$\begin{aligned} r(t, x) &= P(t)r_0(x) + \int_0^t \gamma i(\tau, x)P(t-\tau)d\tau, \\ i(t, x) &= i_0(x)e^{-\gamma t} + \int_0^t s(\tau, x) \left(\int_{-\infty}^{\infty} k(x-y)i(\tau, y)dy \right) e^{-\gamma(t-\tau)}d\tau. \end{aligned} \quad (4.1)$$

The initially removed individuals $r_0(x)$ have left the removed class by time ω , so that $r(t, x) = \int_{t-\omega}^t \gamma i(\tau, x)d\tau$ for $t > \omega$. Note that $i(t, x)$ satisfies the differential equation $\frac{\partial i}{\partial t} = s(t, x) \left(\int_{-\infty}^{\infty} k(x-y)i(t, y)dy \right) - \gamma i$. With $s(t, x) = 1 - i(t, x) - r(t, x)$ and the diffusion approximation (3.2), the model reduces to

$$\frac{\partial i}{\partial t} = \left(1 - i - \int_{t-\omega}^t \gamma i(\tau, x)d\tau \right) \left(\beta i + D \frac{\partial^2 i}{\partial x^2} \right) - \gamma i \quad (4.2)$$

for $t > \omega$.

We are looking for traveling wave solutions, so we assume that $i(t, x) = f(x + ct) = f(\xi)$ with $\xi = x + ct$. This leads to

$$\begin{aligned} cf'(\xi) &= \left(1 - f(\xi) - \int_{t-\omega}^t \gamma f(x + c\tau)d\tau \right) (\beta f(\xi) + Df''(\xi)) - \gamma f(\xi) \\ &= \left(1 - f(\xi) - \frac{\gamma}{c} \int_{\xi-c\omega}^{\xi} f(\eta)d\eta \right) (\beta f(\xi) + Df''(\xi)) - \gamma f(\xi). \end{aligned}$$

Let $f' = u$, so that $u' = f''$, which leads to the two dimensional system of functional differential equations given by

$$\begin{aligned} f' &= u, \\ u' &= \frac{cu + \gamma f}{D \left(1 - f - \frac{\gamma}{c} \int_{\xi-c\omega}^{\xi} f(\eta)d\eta \right)} - \frac{\beta f}{D}. \end{aligned} \quad (4.3)$$

The equilibrium points are the disease-free equilibrium at the origin and the endemic equilibrium given by

$$\begin{pmatrix} f \\ u \end{pmatrix} = \begin{pmatrix} \frac{1-1/\sigma}{1+q} \\ 0 \end{pmatrix},$$

where $\sigma = \beta/\gamma$ is the contact number and $q = \omega\gamma = \omega/(1/\gamma)$ is the ratio of the delay ω in the recovered class to the average infectious period $1/\gamma$. The endemic equilibrium is in the positive half plane $f > 0$, if the contact number σ satisfies $\sigma > 1$.

The linearization of (4.3) at the origin is the same as the linearization of (3.4) so it also has eigenvalues given by (3.6). When $\sigma > 1$, then the discriminant is positive and both eigenvalues are positive real numbers, so that the origin is an unstable node. As in the model in Section 3 without a delay, there is a repulsive direction away from the origin for $c \geq c_{\min} = 2\sqrt{D\gamma(\sigma - 1)}$. If the endemic equilibrium has an attractive direction in the region in which $u > 0$ and f is less than the endemic value, then a heteroclinic orbit joining the origin and the endemic equilibrium would correspond to a traveling wave solution. We do not use this phase plane analysis approach, because we are interested in periodic traveling wave solutions. Note that periodic traveling waves correspond to periodic solutions in the phase plane.

If there is a periodic solution with $f(\xi + P) = f(\xi)$ around the endemic equilibrium in the positive half plane $f > 0$, then it corresponds to a periodic traveling wave solution. In this case the traveling wave would have a period $T = P/c$. Thus we seek periodic solutions arising around the endemic equilibrium by Hopf bifurcation. The conditions for Hopf bifurcation in a functional differential equations are analogous to those stated in Section 3 for differential equations [18, 23, 53].

Translate the endemic equilibrium to the origin by letting

$$x(\xi) = f(\xi) - (1 - 1/\sigma)/(1 + q).$$

From (4.3) we obtain

$$\begin{aligned} x'(\xi) &= u, \\ u'(\xi) &= \frac{cu + \gamma x + \frac{\beta(1-1/\sigma)}{1+q}x + \frac{\gamma}{c} \frac{\beta(1-1/\sigma)}{1+q} \int_{-c\omega}^0 x(\xi + \nu) d\nu}{D \left(\frac{1}{\sigma} - x - \frac{\gamma}{c} \int_{-c\omega}^0 x(\xi + \nu) d\nu \right)} - \frac{\beta x}{D}. \end{aligned}$$

Let $\xi = c\omega\eta$, $x(\xi) = X(\eta)$, and $u(\xi) = U(\eta)$ to obtain that

$$\begin{aligned} X'(\eta) &= c\omega U(\eta), \\ U'(\eta) &= c\omega \frac{cU + \gamma X + \frac{\beta(1-1/\sigma)}{1+q}X + q \frac{\beta(1-1/\sigma)}{1+q} \int_{-1}^0 X(\eta + \nu) d\nu}{D \left(\frac{1}{\sigma} - X - q \int_{-1}^0 X(\eta + \nu) d\nu \right)} - \frac{\beta X}{D}. \end{aligned}$$

Now we linearize the equations for (X, U) at the endemic equilibrium $(0, 0)$

and simplify to obtain

$$\begin{aligned} X'(\eta) &= c\omega U(\eta), \\ U'(\eta) &= \frac{c^2\omega}{D} \sigma U + \frac{cq\sigma(\sigma-1)}{D(1+q)} X + \frac{cq^2\sigma(\sigma-1)}{D(1+q)} \int_{-1}^0 X(\eta + \nu) d\nu. \end{aligned}$$

We substitute $X(\eta) = v_1 e^{\lambda\eta}$ and $U(\eta) = v_2 e^{\lambda\eta}$ into the above linearized the equations to obtain

$$\begin{aligned} v_1 &= c\omega v_2 / \lambda, \\ \lambda v_2 &= \frac{c^2\omega\sigma}{D} v_2 + \frac{cq\sigma(\sigma-1)}{D(1+q)} v_1 + \frac{cq^2\sigma(\sigma-1)}{D(1+q)} v_1 e^{\lambda\eta} \int_{-1}^0 e^{\lambda\nu} d\nu. \end{aligned}$$

These equations can be simplified to obtain the characteristic equation

$$\lambda^3 - \frac{\sigma q}{B} \lambda^2 - \frac{\sigma(\sigma-1)q^2}{B(1+q)} \lambda - \frac{\sigma(\sigma-1)q^3}{B(1+q)} (1 - e^{-\lambda}) = 0, \quad (4.4)$$

where $B = \gamma D / c^2$.

To get Hopf bifurcation, we look for pure imaginary roots of (4.4). Let $\lambda = i\mu$, $\mu > 0$. The real and imaginary parts of equation (4.4) are

$$\mu^2 = \frac{(\sigma - 1)q^2}{(1 + q)}(1 - \cos \mu) \text{ and } \mu^3 + \frac{\sigma(\sigma - 1)q^2}{B(1 + q)}\mu + \frac{\sigma(\sigma - 1)q^3}{B(1 + q)}\sin \mu = 0. \quad (4.5)$$

Solving the first equation in (4.5) for σ , we obtain

$$\sigma = 1 + \frac{(1 + q)\mu^2}{(1 - \cos \mu)q^2}. \quad (4.6)$$

Substituting (4.6) into the second equation in (4.5) and then solving for B , we obtain

$$B = \frac{\left(1 + \frac{(1 - \cos \mu)q^2}{(1 + q)\mu^2}\right)(1 + q)\mu}{q^2(1 - \cos \mu)^2}(-q \sin \mu - \mu) \quad (4.7)$$

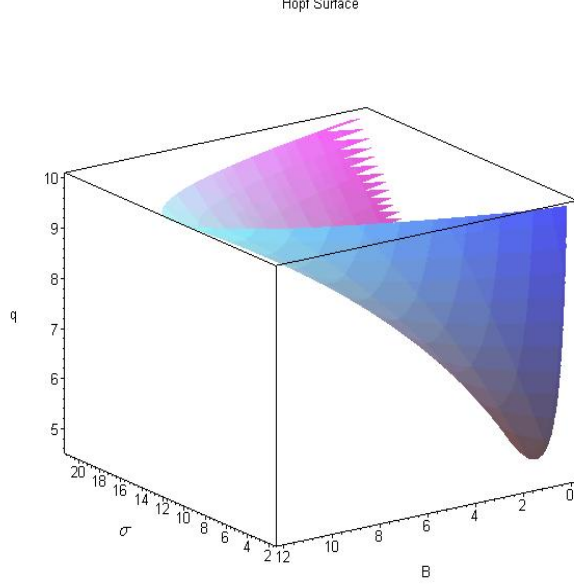
It can easily be seen that solutions of equations (4.6) and (4.7) do exist for certain q and for certain μ . Positive solutions for σ and B can be obtained provided that

$$\frac{\mu}{-\sin \mu} < q. \quad (4.8)$$

This in turn requires that

$$\sin \mu < 0, \quad q = \omega\gamma > \min_{w>0} \left| \frac{w}{\sin w} \right| \approx 4.6. \quad (4.9)$$

Thus for q and μ satisfying (4.9), the characteristic equation (4.4) has purely imaginary roots. The numerical graph of the Hopf bifurcation surface in the (q, σ, B) space is shown here.



We now prove that on the pure imaginary root surface, the transversality condition is satisfied. Indeed, we derive the following for $\lambda = \nu + i\mu$ on the Hopf surface where $\nu = 0$ and (μ, q, σ, B) satisfies (4.6), (4.7) and (4.9):

$$\frac{\partial \nu}{\partial B} = -\frac{q^3(1 - \cos \mu)^2}{1 + q + \frac{(1 - \cos \mu)q^2}{\mu^2}} (-\mu \sin \mu + 2(1 - \cos \mu)) < 0. \quad (4.10)$$

Therefore the roots of the characteristic equation (4.4) cross this pure-imaginary surface. Thus Hopf bifurcation occurs in the system of functional differential equations (4.3) at some values of q and μ satisfying (4.9). Condition (4.9) implies that $q = \omega\gamma = \omega/(1/\gamma)$, the quotient of the delay ω in the recovered class and the average infectious period $1/\gamma$ must be sufficiently large for Hopf bifurcation to occur. When condition (4.9) is satisfied, there exist periodic traveling waves of our diffusion-approximation model (4.2) with a delay in the removed class.

Note that when the characteristic equation (4.4) is multiplied by D and then let $D = 0$, the equations in (4.5) are reduced to the equations for the real and imaginary parts for the non-spatial SIRS model with a delay in the removed class [23]. In fact, the second equation in (4.5) is reduced to

$$\frac{\mu}{-\sin \mu} = q,$$

which is (3.4) in [23]. There were imaginary root curves for the reduced characteristic equation. For our spatial SIRS model with a delay in the removed class (4.2) in which $D > 0$, the condition above is replaced by (4.8) and there is an imaginary root surface for characteristic equation (4.4). From the graph of the Hopf bifurcation surface, we see that the region in (q, σ) plane in which oscillatory solutions occur gets smaller as the scaled diffusion coefficient $B = \frac{\gamma D}{c^2}$ increases. Indeed, on the Hopf surface, we could regard (q, σ) as functions of (B, μ) . In doing so we find the following:

$$\begin{aligned} \frac{\partial \sigma}{\partial B} &= -\frac{(q+2)(1-\cos \mu)\mu^3}{-\sin \mu(1-\cos \mu)q^3 + \mu^2(\mu + \sin \mu)q + 2\mu^3} \\ \frac{\partial q}{\partial B} &= \frac{q^3(1-\cos \mu)^2\mu}{-\sin \mu(1-\cos \mu)q^3 + \mu^2(\mu + \sin \mu)q + 2\mu^3}. \end{aligned}$$

Since $\sin \mu < 0$ and $\mu > 0$ on the surface we have that $\mu + \sin \mu > 0$ and $\frac{\partial \sigma}{\partial B} < 0$, and $\frac{\partial q}{\partial B} > 0$, which shows that the surface becomes higher in q and narrower in σ as B increases. Thus dispersal decreases the range of parameters over which the solution is oscillatory.

5 Discussion

We conjecture that an infectious disease could remain endemic by traveling geographically around a region or continent, so that it would encounter a fresh supply of susceptibles each time that it returned to a location. In order to investigate this possibility, we have considered distributed-contacts, spatial epidemiology models, which are generalizations of some non-spatial endemic models of SIRS type. We have shown that periodic traveling infection wave fronts do not arise by Hopf bifurcation for the spatial analog of the usual SIRS endemic model with exponential waiting times in I and R . Because the nonexistence of periodic traveling waves in the spatial SIRS model is connected to the nonexistence of periodic solutions in the analogous non-spatial SIRS endemic model, we conjecture that this connection would exist for other endemic models. For example, the non-spatial SIRS endemic model with vital dynamics (births and deaths) and exponential waiting times in I and R does not have periodic solutions [19], so we do not expect the analogous spatial SIRS model with diffusion-distributed contacts to have periodic solutions. However, some preliminary calculations for the similar spatial SIRS model with a higher order diffusion approximation given by

$$\int_{-\infty}^{\infty} k(x-y)i(t,y)dy \approx \beta i(t,x) + D \frac{\partial^2 i(t,x)}{\partial x^2} + C \frac{\partial^4 i(t,x)}{\partial x^4}$$

with $C \neq 0$ suggests that periodic traveling waves can arise by Hopf bifurcation. Thus the conjecture above may apply only to the spatial models with simple diffusion-distributed contacts.

For the spatial analog of an SIRS endemic model in which the temporary immunity is described by a delay, we have shown that periodic traveling infection wave fronts do arise by Hopf bifurcation around the endemic equilibrium. Moreover, the parameter region in which oscillatory solutions occur decreases in size as the diffusion coefficient increases. These periodic traveling wave solutions are related to the periodic solutions found for a non-spatial SIRS model with a delay in the R class [23].

The simple mass action law $\eta IS = \eta(Ni)(Ns)$, with η as a mass action coefficient, is sometimes used for the incidence, but the parameter η does not have an epidemiological interpretation [2, 21]. The standard form of the incidence is more consistent with epidemiological data than the simple mass action incidence [1, p. 157] [2, p. 306] [21]. Various forms of nonlinear incidences such as $\beta(I/N)^p S$ have been considered [26, 34, 35, 36]. Because the periodic traveling waves in the spatial SIRS model with a delay in the R compartment arise from the occurrence of oscillation in the analogous to the non-spatial SIRS model with a delay in R [23], we conjecture that this connection would exist for other endemic models. Since nonlinear incidence in non-spatial endemic models leads to periodic solutions [22, 34, 35], we conjecture that periodic traveling infection waves would arise for the spatial analog of an SIRS endemic model with nonlinear incidence of the form $\int_{-\infty}^{\infty} k(x-y)i^p(t,y)dy$ with $p > 1$. See [22] for a survey of mechanisms that can lead to periodicity in non-spatial epidemiological models.

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