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Two SIS epidemiologic models with delays

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Abstract. The SIS epidemiologic models have a delay corresponding to the infectious period, and disease-related deaths, so that the population size is variable. The population dynamics structures are either logistic or recruitment with natural deaths. Here the thresholds and equilibria are determined, and stabilities are examined. In a similar SIS model with exponential population dynamics, the delay destabilized the endemic equilibrium and led to periodic solutions. In the model with logistic dynamics, periodic solutions in the infectious fraction can occur as the population approaches extinction for a small set of parameter values.

Key words: Epidemiologic modeling – SIS model – Delay – Threshold – Hopf bifurcation

1. Introduction

Delays in population dynamics models can destabilize an equilibrium, so that periodic solutions arise by Hopf bifurcation. In SIS epidemiologic models, susceptibles become infectious after sufficient contact with an infective and then become susceptible again after they have recovered from the infection. For the SIS model with exponential population dynamics in [11], changing to a delay for the infectious period does destabilize the endemic equilibrium for a small parameter

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set and leads to periodic solutions in the infectious fraction as the population size approaches extinction. In this paper we complete our study of the simple SIS models with delays and variable population size by considering the SIS models with disease-related deaths and either recruitment with natural deaths or generalized logistic growth. These two population dynamics structures with limited growth are more realistic than the exponential growth structure.

The passage time of a person in the infective class is defined by means of a survival probability function $P(t)$, which is the probability of still being infectious t time units after becoming infectious [9]. When $P(t)$ corresponds to a negative exponential distribution, the models reduce to systems of ordinary differential equations. Here the SIS models are formulated with distributed delays corresponding to a general $P(t)$, and the thresholds and equilibria are determined. The stabilities of the endemic equilibria are difficult to analyze, but some stability results are obtained for a general $P(t)$ or in the case when $P(t)$ is a step function corresponding to a fixed infectious period for every infective. The SIS models here consist of systems of two integral equations for the infectious fraction and the population size, or their equivalent system of delay-integro-differential equations.

Models with variable population size are interesting for several reasons. Instead of one threshold given by the basic reproduction number, these models can involve several thresholds that determine the asymptotic behavior. Moreover, the combination of the epidemiologic and demographic processes can yield new behaviors that do not occur in epidemiologic models with constant population size. For example, when the disease persists, the disease-related deaths and the reduced reproduction of infectives can reduce the growth rate or change a growing population into a population with a stable size or a decreasing size [1, 8]. A disease is said to persist or remain endemic in a population if the infectious fraction of the population is bounded away from zero. In a population decaying to zero with the number of infectives going to zero, the disease would still persist if the infectious fraction is bounded away from zero.

Some variable population models with a delay have been considered previously. The epidemiologic class R consists of those who are removed with immunity. In an SIR model with a maturation period delay during which the newborns do not participate in the horizontal transmission of the disease, periodic solutions occur for some parameter values [5, 4] . In SI, SIS and SIR models with a generalized logistic demographic structure and death or recovery corresponding to a distributed delay, periodic solutions can arise by Hopf bifurcation [2, 3]. In [6] multiple endemic equilibria are shown to be possible in a

distributed delay multi-group model of HIV/AIDS with variable population size. In the SI class-age model of HIV/AIDS in [15] with constant recruitment and disease-related deaths corresponding to a distributed delay, variable infectiousness and population-size dependent incidence are needed to destabilize the endemic equilibrium.

For gonorrhea and some other bacterial agent diseases, people are susceptible as soon as they recover from infection, so that models of SIS type are appropriate [12]. Models of SIS type have also been used for Chagas disease [4, Sect. 3.5–3.6] and Rocky Mountain Spotted Fever [4, Sect. 2.13]; the latter model involves logistic regulation. In SIS models with a time delay in the infectious class and a constant population size, all solutions approach equilibria as $t \to \infty$ [7]. The two SIS models analyzed here differ from previous models, because they have a delay corresponding to the infectious period and limited growth population structures. For the first model with a recruitment-death population structure, there is only one threshold that determines the asymptotic behavior. But for the second model with a logistic population growth structure, there are two primary threshold quantities that determine the "phase portrait." In a similar SIS model with an exponential population dynamics, periodic solutions in the infectious fraction can occur for a small parameter set when there is a delay corresponding to the infectious class [11]. Similar periodic solutions in the infectious fraction are found for the SIS model with logistic growth.

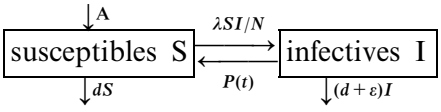
2. Formulation of model 1: recruitment-death structure

A population of size $N(t)$ at time t is divided into susceptible and infectious individuals with the numbers in these epidemiologic classes given by $S(t)$ and $I(t)$, respectively, so that

$$N(t) = S(t) + I(t). \tag{1}$$

The inflow of new susceptibles due to immigration or recruitment is given by a positive constant rate A. The natural death rate constant d is positive and the disease-related death rate constant ε is nonnegative. In the absence of disease, the differential equation for the population size N is $N'(t) = A - dN$, so that $N(t)$ approaches A/d for any nonzero initial population size. The positive contact rate constant λ is the average number of adequate contacts of an infective per unit time, so that $\lambda S/N$ is the average number of adequate contacts (sufficient for transmission of the infection) with susceptibles of one infective per unit time, and $\lambda SI/N$ is the incidence, that is, the number of new cases per unit time.

For $t \geqq 0$, let $P(t)$ be the fraction of infectives remaining in the infective class t time units after becoming infected. Here $P(t)$ is assumed to be nonnegative, non-increasing, and piecewise continuous with $P(0^+) = 1$ and $\int_0^\infty P(u)\,du = \omega$. The mean length (ignoring death processes) of infection ω is assumed to be positive and finite. In the limit as $\omega \to \infty$, individuals do not recover from the disease, so that the SIS model becomes an SI model. The SIS model with a general $P(t)$ is shown to be well posed, and the thresholds and equilibria are found. Then the asymptotic behaviors are examined for the model with a step function $P(t)$ corresponding to a constant period of infection. The transfer diagram for this SIS model is given below.



For $t \geqq 0$, the integral equation for the number of infectives $I(t)$ is:

$$I(t) = I_0(t) + \int_0^t \lambda[(N(u) - I(u))\,I(u)/N(u)]\,P(t-u)\,e^{-(d+\varepsilon)(t-u)}\,du, \tag{2}$$

where we have used $S = N - I$. The integral in (2) is the summation up to time t of those who became infected at time u and who have neither recovered back to the susceptible class nor died from natural or disease-related causes in the time interval $[u, t]$. Here $I_0(t)$ is the number of infectives who were in the infectious class at time 0 and are still infectious at time t. This function $I_0(t)$ is a non-negative, non-increasing, piecewise continuous function that satisfies

$$I_0(t) \leqq I_0(0)\,e^{-(d+\varepsilon)t} \max_{u \geqq 0}[P(t+u)/P(u)].$$

Note that $\max_{u \geqq 0}[P(t+u)/P(u)]$ corresponds to considering all possible times of infection that would yield an infectious group at time t. The integral equation (2) and the inequality above for $I_0(t)$ could also be derived by using the infection-class-age approach as done in Sect. 6 for the second model where the death rate constant d is generalized to $D(N)$. Observe that the condition $I_0(t) \leqq I_0(0)\,P(t)\,e^{-(d+\varepsilon)t}$ used in [11] and other papers works when $P(t)$ is an exponential or a delay function, but it does not work for the function $P(t)$ equal to 1 on $[0, \omega/2]$, $1/2$ on $(\omega/2, 3\omega/2]$, and 0 on $(3\omega/2, \infty)$.

The assumptions above and the transfer diagram lead to the differential equation

$$N'(t) = A - dN - \varepsilon I, \tag{3}$$

where $N(0) > 0$ and $N(0) \geqq I_0(0)$. An equivalent integral equation is

$$N(t) = N(0)\,\mathrm{e}^{-dt} + \int_0^t [A - \varepsilon I(u)]\,\mathrm{e}^{-d(t-u)}\,du. \tag{4}$$

Note that the model given by (2) and (3) is a hybrid system consisting of one integral equation and one differential equation, but (2) and (4) are an equivalent system of two integral equations.

Consider the infinite wedge region defined by $0 \leqq I \leqq N$ in (I, N) space. At the bottom corner where $N = I = 0$, $N' = A > 0$, so that solution paths move away from this point where the quotient $\lambda SI/N$ is discontinuous. Consider solutions of the system of integral equations (2) and (4) in the region

$$\mathfrak{D} = \{(I, N) | 0 \leqq I \leqq N, 0 < N\}. \tag{5}$$

In this region the local existence, uniqueness and continuation results follow directly from standard theorems [13]. Namely, there exists a unique solution $(I(t), N(t))$ of (2) and (4) with $N(0) > 0$ that exists on a maximal interval. If the solution remains bounded, then the maximal interval is $[0, \infty)$. The following theorem implies that solutions starting in $\mathfrak{D}$ remain bounded in $\mathfrak{D}$, so that they exist for all time $t \geqq 0$.

Theorem 1. *Consider solutions of* (2) *and* (4) *starting in* $\mathfrak{D}$.

a) *If* $I_0(0) = 0$, *then* $I(t) = 0$ *for all* $t \geqq 0$ *and* $N(t) \to A/d$ *as* $t \to \infty$.
b) *If* $N(0) > I_0(0) > 0$, *then solutions remain bounded and* $N(t) > I(t) > 0$ *for all finite* $t \geqq 0$.
c) *If* $N(0) = I_0(0) > 0$, *then solutions remain bounded and* $N(t) > I(t) > 0$ *for all finite* $t > 0$.

Proof. Assertion a) follows from uniqueness and equation (3). The quotient $\lambda SI/N$ is sufficiently smooth near an initial point in $\mathfrak{D}$ that the theorems cited above imply that a solution exists on some maximal interval. For assertion b) let $T = \inf\{t > 0 | (N(t) - I(t))\, I(t)/N(t) = 0\}$ and suppose that T is finite. The terms on the right in (2) are non-negative and the integral is positive since $(N(t) - I(t))I(t)/N(t) > 0$ on $[0, T)$, so that $I(t) > 0$ on $[0, T]$. On $[0, T]$ equation (3) implies that $N'(t) < A - dN$, so that $N(t)$ is decreasing at t if $N(t) \geqq A/d$. Thus $N(t) \leqq \max\{A/d, N(0)\}$ on $[0, T]$. Note that $S(0) = N(0) - I(0) > 0$, and that $S(t) = N(t) - I(t) > 0$ on $[0, T)$. The assumptions in the model imply that on $[0, T)$, $S'(t) \geqq -dS - \lambda SI/N \geqq -(d + \lambda)S$, so that $N(T) - I(T) = S(T) \geqq S(0)\,\mathrm{e}^{-(d+\lambda)T} > 0$. Because $N(T)$ is finite, $(N(T) - I(T))I(T)/N(T) > 0$. This contradicts the supposition that T is finite, so T must be infinite. Hence $N(t) - I(t) = S(t) > 0$ and $I(t) > 0$ for all $t \geqq 0$.

Suppose that assertion c) is false, so that $I(t) \geqq N(t)$ on $[0, T)$ for some $T > 0$. Then the second term on the right in (2) is non-positive, so that

$$I(t) \leqq I_0(t) \leqq I_0(0)\, e^{-(d+\varepsilon)t} = N(0)\, e^{-(d+\varepsilon)t},$$

since $\max_{u \geqq 0}[P(t+u)/P(u)] \leqq 1$ and $I_0(0) = N(0)$. On $[0, T)$ equation (3) implies that $N'(t) \geqq A - dN - \varepsilon N(0)\, e^{-(d+\varepsilon)t}$. Integrating this differential inequality leads to

$$N(t) \geqq A(1 - e^{-dt})/d + N(0)\, e^{-(d+\varepsilon)t} > N(0)\, e^{-(d+\varepsilon)t} = I_0(0)\, e^{-(d+\varepsilon)t}$$

$$\geqq I_0(t) \geqq I(t).$$

This strict inequality contradicts the supposition above, so that $N(t) > I(t)$ on some interval $(0, T)$. Assertion c) then follows from part b). □

The special case when the waiting time is exponentially distributed with $P(t) = \exp(-\gamma t)$ and mean $\gamma = 1/\omega$ is equivalent to removal from the infectious class I at rate γI [10]. In this case, $I_0(t) = I_0(0)\exp[-(\gamma + d + \varepsilon)\, t]$ and the integral equation (2) reduces to the differential equation $I' = \lambda SI/N - (\gamma + d + \varepsilon)I$. This special case was analyzed in [16].

In the special case when all individuals have a constant length of infection ω, $P(t)$ is a step function with $P(t) = 1$ on $[0, \omega]$ and 0 on (ω, ∞). The initial infectives must have recovered by time ω, so that $I_0(t) = 0$ for $t \geqq \omega$. In this case the integral equation (2) for $t \geqq \omega$ becomes

$$I(t) = \int_{t-\omega}^{t} \lambda[(N(u) - I(u))I(u)/N(u)]\, e^{-(d+\varepsilon)(t-u)}\, du, \tag{6}$$

which is equivalent to the delay-differential equation

$$I'(t) = \lambda(N(t) - I(t))I(t)/N(t) - \lambda[(N(t-\omega)$$

$$- I(t-\omega))I(t-\omega)/N(t-\omega)]\, e^{-(d+\varepsilon)\omega} - (d+\varepsilon)I(t). \tag{7}$$

3. The threshold and the two equilibria for model 1

The survival probability in the integral equation (2) is $Q(t) = P(t)\exp(-(d+\varepsilon)\, t)$, so that the mean passage time or expected time

in the I class during one passage is

$$\bar{t} = \int_0^\infty t(-Q'(t))\,dt = \int_0^\infty Q(t)\,dt = \int_0^\infty P(t)\,e^{-(d+\varepsilon)t}\,dt. \tag{8}$$

The basic reproduction number is the average number of new cases in the limiting situation when everyone is susceptible. Here the basic reproduction number $R_0 = \lambda\bar{t}$ (sometimes called the contact number) is the product of the contact rate per unit time and the average number of time units spent in the infectious class. For the step function $P(t)$, the basic reproduction number is

$$R_0 = \lambda\,\frac{1 - e^{-(d+\varepsilon)\omega}}{d+\varepsilon}. \tag{9}$$

The equilibria in $\mathfrak{D}$ are given in the following theorem. Note that the reproduction number (sometimes called the infective replacement number) $R_0 S_e/N_e$ is 1 at the endemic equilibrium.

Theorem 2. *The model given by* (2) *and* (3) *always has the disease free equilibrium* $(I, N) = (0, A/d)$. *If* $R_0 \leqq 1$, *then it has no other equilibria. If* $R_0 > 1$, *then it also has a unique endemic equilibrium given by*

$$(I_e, N_e) = \left(\frac{(R_0 - 1)\,A}{R_0 d + (R_0 - 1)\,\varepsilon}, \frac{R_0 A}{R_0 d + (R_0 - 1)\,\varepsilon}\right). \tag{10}$$

4. Stability of the disease free equilibrium in model 1

The disease free equilibrium is globally asymptotically stable below the threshold, but is unstable above it.

Theorem 3. *Assume that* $P(t)$ *has compact support* $[0, a]$ *in the model given by* (2) *and* (3). *If* $R_0 < 1$, *then the disease free equilibrium* $(0, A/d)$ *is globally asymptotically stable in* $\mathfrak{D}$; *if* $R_0 > 1$, *then it is unstable.*

Proof. Let $M = \max\{N(0), A/d\}$, so that $I(t) \leqq M$ for $t \geqq 0$ from Theorem 1b. Note that $I_0(t)$ also has compact support $[0, a]$. Using $S(u)/N(u) \leqq 1$, and $I(u) \leqq M$ in (2) yields $I(t) \leqq MR_0$ for $t > a$. Using this inequality in (2) yields $I(t) \leqq MR_0^2$ for $t \geqq 2a$. By induction $I(t) \leqq MR_0^n$ for $t \geqq na$, so that $I(t) \to 0$ as $t \to \infty$. When $I(t) \to 0$, equation (3) is asymptotically equivalent to $N' = A - dN$, so $N(t) \to A/d$ as $t \to \infty$.

Local stability for a system of integral equations is determined by analyzing the characteristic equation obtained by linearization around the equilibrium [13]. Linearize equations (2) with $I_0(t) = 0$ and (3),

which is equivalent to the integral equation (4) for N, around the disease free equilibrium using $N = A/d + V$ to obtain

$$I(t) = \int_0^t \lambda I(u) P(t-u) \, e^{-(d+\varepsilon)(t-u)} \, du,$$

$$V'(t) = -dV - \varepsilon I.$$

Using $I = c_1 e^{zt}$ and $V = c_2 e^{zt}$ leads to the root $z = -d$ and the characteristic equation

$$1 = \lambda \int_0^\infty P(v) \, e^{-(z+d+\varepsilon)v} \, dv. \tag{11}$$

For $R_0 > 1$, look for a real root with $z = x > 0$. Then the right side of (11) is a decreasing function of x from $R_0 > 1$ at $x = 0$ to zero as x approaches infinity. Hence there is a positive real root x if $R_0 > 1$ and the disease free equilibrium is like an unstable saddle, which has the N axis as its attractive manifold. □

5. Stability of the endemic equilibrium in model 1

Consider the endemic equilibrium given by (10), which exists in $\mathfrak{D}$ for $R_0 > 1$. The proof below that the endemic equilibrium is locally asymptotically stable under certain conditions excludes the possibility that a periodic solution arises by Hopf bifurcation under these conditions. We have not been able to find periodic solutions numerically under any conditions. Consequently, we conjecture that the endemic equilibrium is globally asymptotically stable in $\mathfrak{D}$ when $I_0(0) > 0$.

Theorem 4. *Assume that $P(t)$ is a step function on $[0, \omega]$. If $R_0 > 2$, or $1 < R_0 < 2$ and $d(3 - R_0) \geqq \varepsilon(R_0 - 1)^2/R_0$, then the endemic equilibrium (I_e, N_e) is locally asymptotically stable.*

Proof. Linearize equations (6) and (3) around the endemic equilibrium using $I = I_e + U$ and $N = N_e + V$ to obtain

$$U(t) = \lambda \int_{t-\omega}^t [(1 - 1/R_0)^2 V(u) + (2/R_0 - 1) U(u)] \, e^{-(d+\varepsilon)(t-u)} \, du,$$

$$V' = -dV - \varepsilon U.$$

Using $U = c_1 e^{zt}$ and $V = c_2 e^{zt}$ leads to $c_1\varepsilon + c_2(z+d) = 0$ and

$$c_1\left[1 - \left(\frac{2}{R_0} - 1\right)\lambda\,\frac{1 - \mathrm{e}^{-(z+d+\varepsilon)\omega}}{z+d+\varepsilon}\right] - c_2\left(1 - \frac{1}{R_0}\right)^2 \times \lambda\,\frac{1 - \mathrm{e}^{-(z+d+\varepsilon)\omega}}{z+d+\varepsilon} = 0. \tag{12}$$

This system has a nontrivial solution iff the determinant of the coefficients is zero, which gives the characteristic equation

$$z + d + \left[(z+d)\left(1 - \frac{2}{R_0}\right) + \varepsilon\left(1 - \frac{1}{R_0}\right)^2\right]\lambda\,\frac{1 - \mathrm{e}^{-(z+d+\varepsilon)\omega}}{z+d+\varepsilon} = 0. \tag{13}$$

It is proved below that there are no purely imaginary roots for $R_0 \geqq 2$, and that there are no roots with nonnegative real parts for $1 < R_0 < 2$ and $d(3 - R_0) \geqq \varepsilon(R_0 - 1)^2$. The characteristic equation (13) is in the form considered in Theorem A.1 in [11], so that all roots with $\mathrm{Re}(z) \geqq 0$ lie in a bounded domain. Because roots cannot enter the parameter region where $\mathrm{Re}(z) \geqq 0$ by crossing the imaginary root surface and roots cannot enter that region from infinity, the continuous dependence of the roots on the coefficients implies that the parameter region with $1 < R_0 \leqq 3$ and $\varepsilon = 0$, where all roots have negative real parts, can be expanded to the parameter region given above. Because all roots of the characteristic equation have negative real parts under the conditions above, the endemic equilibrium is locally asymptotically stable in this parameter region [13].

Note that for $R_0 > 1$, $z = 0$ is not a root of the characteristic equation (13). Suppose that (13) has purely imaginary roots $z = iy$ with $y > 0$. Then the imaginary part of the characteristic equation is

$$0 = y(2d + \varepsilon) + y\lambda\left(1 - \frac{2}{R_0}\right)[1 - \mathrm{e}^{-(d+\varepsilon)\omega}\cos y\omega] + \lambda\left[d\left(1 - \frac{2}{R_0}\right) + \varepsilon\left(1 - \frac{1}{R_0}\right)^2\right]\mathrm{e}^{-(d+\varepsilon)\omega}\sin y\omega. \tag{14}$$

First consider the parameter region with $R_0 \geqq 2$. Using $\lambda = (d+\varepsilon)R_0/(1 - \mathrm{e}^{-(d+\varepsilon)\omega})$ from (9), $D = d\omega$, $E = \varepsilon\omega$, and $Y = y\omega$ in (14) yields

$$0 = Y(2D + E)[1 - e^{-D-E}] + Y(D+E)(R_0 - 2)[1 - e^{-D-E}\cos Y] + (D+E)[(D+E)(R_0 - 2) + E/R_0]e^{-D-E}\sin Y.$$

After dividing by Y, this can be rearranged as

$$0 = (2D + E)\,e^{-D-E}[e^{D+E} - 1] + (D + E)(E/R_0)\,e^{-D-E}\sin Y/Y$$
$$+ (D + E)\,(R_0 - 2)\,e^{-D-E}[e^{D+E} - \cos Y + (D + E)\sin Y/Y].$$

Now $R_0 \geqq 2$, $-\cos Y \geqq -1$, $\sin Y/Y \geqq -1$, and $e^{D+E} \geqq 1 + (D + E)$ imply that

$$0 \geqq (D + E)\,e^{-D-E}[(D + E) - E/2] + (D + E)(R_0 - 2)$$
$$\times e^{-D-E}[1 + (D + E) - 1 - (D + E)] > 0,$$

which is a contradiction. Thus for $R_0 \geqq 2$, there are no purely imaginary roots, since (14) cannot be satisfied.

For $1 < R_0 < 2$, rewrite the characteristic equation (13) as

$$z + d = \left[(z + d)\left(\frac{2}{R_0} - 1\right) - \varepsilon\left(1 - \frac{1}{R_0}\right)^2\right]\int_{-\omega}^{0} \lambda e^{(z+d+\varepsilon)u}\,du.$$

Let $z = x + iy$ with $x \geqq 0$ and take absolute values of the equation above to obtain

$$|x + d + iy| \leqq \left|(x + d)\left(\frac{2}{R_0} - 1\right) - \varepsilon\left(1 - \frac{1}{R_0}\right)^2 + iy\left(\frac{2}{R_0} - 1\right)\right|$$
$$\times \int_{-\omega}^{0} \lambda e^{(d+\varepsilon)u}\,du.$$

The integral in the equation above is R_0, so that

$$(x + d)^2 + y^2 \leqq [(x + d)(2 - R_0) - \varepsilon(R_0 - 1)^2/R_0]^2 + [y(2 - R_0)]^2.$$

The terms on the left are greater than the terms on the right if $1 < R_0 < 2$, and

$$-(x + d) \leqq (x + d)(2 - R_0) - \varepsilon(R_0 - 1)^2/R_0 \leqq (x + d). \qquad (15)$$

In (15) the right inequality always holds and the left inequality holds for $x \geqq 0$ if $d(3 - R_0) \geqq \varepsilon(R_0 - 1)^2/R_0$. This contradiction proves that there are no roots with non-negative real parts under the given conditions. For $\varepsilon = 0$, the inequalities in (15) hold for $1 < R_0 \leqq 3$, so in this case there are no roots with non-negative real parts. □

6. Formulation of model 2: generalized logistic structure

The standard equation for restricted growth in a population is the logistic differential equation $N'(t) = r(1 - N/K)\,N$. In an analysis of an

SIRS model [8], the logistic equation has been written in the form

$$N'(t) = (b - arN/K)\,N - (d + (1 - a)\,rN/K)\,N, \tag{16}$$

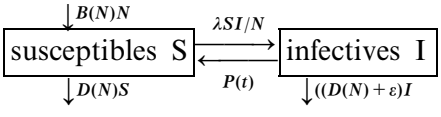
with $0 \leqq a \leqq 1$, where $r = b - d$ is the net growth rate and K is the carrying capacity of the environment. For $0 < a < 1$ the first term in equation (16) has a decreasing birth rate coefficient $b - arN/K$ and the second term has an increasing death rate coefficient $d + (1 - a)\,rN/K$. All of the restricted growth is due to a decreasing birth rate when $a = 1$. When $a = 0$, it is called a logistic death model since all of the restricted growth is due to an increasing death rate and the birth rate constant is b.

An obvious generalization of the logistic equation (16) is the generalized logistic equation

$$N'(t) = [B(N) - D(N)]\,N, \tag{17}$$

where $B(N)$ is the population-size-dependent birth rate coefficient and $D(N)$ is the population-size-dependent death rate coefficient. As in [16] assume that $B(N) - D(N)$ is a strictly decreasing function in $[0, K]$ with $B(K) - D(K) = 0$, that $B(N) - D(N) < 0$ for $N > K$, that the birth function $B(N)$ is a non-increasing, nonnegative function in $C[0, \infty) \cap C'(0, \infty)$, and that the natural death function $D(N)$ is a nonnegative, non-decreasing function in $C[0, \infty) \cap C'(0, \infty)$. These conditions imply that in the absence of disease, the population size N approaches the carrying capacity K if $N(0) > 0$. Since $dN/dt < 0$ for $N > K$, all solution paths in the first quadrant of SI space approach, enter or stay in the subset where $S + I = N \leqq K$, so it suffices to analyze solutions in this subset.

The transfer diagram for this SIS model is given below.



For $t \geqq 0$, the integral equation of the number of infectives $I(t)$ is:

$$I(t) = I_0(t) + \int_0^t \lambda[(N(u) - I(u))I(u)/N(u)]\,P(t - u) \times \exp\left[- \int_u^t [\varepsilon + D(N(p)]\,dp \right] du. \tag{18}$$

The epidemiologic assumptions, the notation, and the interpretation of $I_0(t)$ and the integral in (18) are the same as for the first SIS model in Sect. 2.

An alternate method as in [15] to obtain (18) is to consider the model with an infection-class-age τ, i.e. the time since entering the class of infectives. Consider

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial \tau}\right) i(t,\tau) = -\left[D(N(t))+\varepsilon+\alpha(\tau)\right] i(t,\tau),$$

where $I(t)=\int_0^\infty i(t,\tau)\,d\tau$, the inflow at infection-class-age 0 is $i(t,0)=\lambda S(t)\,I(t)/N(t)$, and $\alpha(\tau)$ is the recovery rate coefficient, so that the proportion of those still in the infective class at infection-class-age τ is $P(\tau)=\mathrm{e}^{-\int_0^\tau \alpha(q)\,dq}$. Integrating along characteristics yields

$$i(t,\tau) = i(t-\tau,0)\,\mathrm{e}^{-\int_{t-\tau}^{t}[\varepsilon+D(N(p))]\,dp-\int_0^\tau \alpha(q)\,dq} \quad \text{for } 0 \leqq \tau \leqq t,$$

$$i(t,\tau) = i(0,\tau-t)\,\mathrm{e}^{-\int_0^t[\varepsilon+D(N(p))]\,dp-\int_{\tau-t}^{\tau}\alpha(q)\,dq} \quad \text{for } t \leqq \tau < \infty.$$

If the interval in the integral for $I(t)$ is divided at t and the solutions above are substituted, then

$$I(t) = \int_0^t i(t-\tau,0)\,\mathrm{e}^{-\int_{t-\tau}^{t}[\varepsilon+D(N(p))]dp-\int_0^\tau \alpha(q)\,dq}\,d\tau$$

$$+\int_t^\infty i(0,\tau-t)\,\mathrm{e}^{-\int_0^t[\varepsilon+D(N(p))]dp-\int_{\tau-t}^{\tau}\alpha(q)dq}\,d\tau.$$

Changing integration variables in these integrals and using $S=N-I$ and the definitions of $i(t,0)$ and $P(\tau)$ leads to

$$I(t) = \int_0^t \frac{\lambda[N(u)-I(u)]\,I(u)}{N(u)}\,\mathrm{e}^{-\int_u^t[\varepsilon+D(N(p))]dp}\,P(t-u)\,du$$

$$+\,\mathrm{e}^{-\int_0^t[\varepsilon+D(N(p))]dp}\int_0^\infty i(0,u)\,\frac{P(t+u)}{P(u)}\,du.$$

This is equivalent to (18) with non-negative, non-increasing, piecewise continuous function $I_0(t)$ given by the second integral above, so that $I_0(t)$ satisfies

$$I_0(t) \leqq I_0(0)\exp\left[-\int_0^t[\varepsilon+D(N(p)]\,dp\right]\max_{u\geqq 0}[P(t+u)/P(u)].$$

Although this infection-class-age approach is a more complicated method for deriving the integral in (18), it does have the advantage that it yields an explicit integral and an upper bound for $I_0(t)$.

The generalized logistic assumptions and the transfer diagram lead to the differential equation

$$N'(t) = [B(N)-D(N)]N-\varepsilon I, \tag{19}$$

where initially $N(0) > 0$ and $N(0) \geqq I_0(0)$. Thus this second model given by (18) and (19) is also a hybrid system consisting of one integral equation and one differential equation.

It is convenient to consider the model with the susceptible fraction $s(t) = S(t)/N(t)$ and infectious fraction $i(t) = I(t)/N(t)$ of the population, so that

$$s(t) + i(t) = 1. \tag{20}$$

With this notation the differential equation (19) becomes

$$N' = [B(N) - D(N) - \varepsilon i]N. \tag{21}$$

From equations (18) and (21), the integral equations for $i(t)$ and $N(t)$ are found to be

$$\begin{aligned} i(t) &= i_0(t) + \int_0^t \lambda[1 - i(u)]\, i(u)\, P(t-u) \\ &\quad \times \exp\left[-\int_u^t [\varepsilon(1 - i(p)) + B(N(p)]dp \right] du, \\ N(t) &= N(0) \exp\left[\int_0^t [B(N(p)) - D(N(p)) - \varepsilon i(p)]\, dp \right], \end{aligned} \tag{22}$$

where $i_0(t) = I_0(t)/N(t)$.

Consider solutions of this equivalent system of integral equations in the region

$$U_K = \{(i, N) | 0 \leqq i \leqq 1, 0 \leqq N \leqq K\}. \tag{23}$$

The region U_K is positively invariant and because of the differential equation for N, all solutions in U_∞ approach, enter or stay in U_K, so it is sufficient to consider solutions in the region U_K. In this region the usual local existence, uniqueness and continuation results apply [13]. Hence there exists a unique solution $(i(t), N(t))$ of (22) with $N(0) > 0$ that exists on a maximal interval, which is $[0, \infty)$ if the solution remains bounded. The following theorem implies that solutions starting in U_K remain bounded in U_K, so that they exist for all time $t \geqq 0$.

Theorem 5. *Consider solutions of* (22) *starting in* U_K *with* $N(0) > 0$.

a) *If* $i_0(0) = 0$, *then* $i_0(t) = 0$ *for all* $t \geqq 0$ *and* $N(t) \to K$ *as* $t \to \infty$.

b) *If* $1 > i_0(0) > 0$, *then* $N(t) > 0$ *and* $1 > i(t) > 0$ *for all finite* $t \geqq 0$.

Proof. Assertion a) follows from uniqueness of solutions of equations (22). For assertion b), note that by the assumptions on $I_0(t)$, $i_0(t)$ is a nonnegative function in $[0, 1]$ with $1 > i_0(0) > 0$. Let $T = \inf\{t > 0 | s(t)i(t) = 0\}$ and suppose that T is finite. The terms on

the right in the first equation in (22) are nonnegative and the integral is positive if $s(t)\, i(t) > 0$ on $[0, T)$, so that $i(T) > 0$. The assumptions in the model imply that $s'(t) \geqq -B(K)\, s - \lambda si \geqq -(B(K) + \lambda)\, s$, so that $s(T) \geqq s(0)\, e^{-(B(K)+\lambda)T} > 0$, since $s(0) = 1 - i_0(0) > 0$. This contradicts the supposition that T is finite, so T must be infinite. Hence $1 > i(t) > 0$ for all $t \geqq 0$. Note that although both $N(t)$ and $i(t)$ are positive for all $t \geqq 0$, they can approach zero as t approaches infinity. □

The special case when the waiting time is exponentially distributed with $P(t) = \exp(-\gamma t)$ and mean $\gamma = 1/\omega$ is equivalent to removal from the infectious class I at rate γI [10]. In order to be consistent with this assumption, the initial infectives satisfy

$$I_0(t) = I_0(0) \exp\left[-\int_0^t [\gamma + \varepsilon + D(N(p))]\, dp \right]$$

and $i_0(t) = i_0(0) \exp[-\int_0^t [\gamma + \varepsilon(1 - i(p)) + B(N(p))] dp]$. In this case, the i integral equation (22) reduces to the differential equation $i' = (\lambda - \varepsilon)(1 - i)\, i - [\gamma + B(N(t))] i$. This is a special case of a more general model analyzed completely in [16]. Here we consider the model with a constant length infectious period; we compare with this differential equations model in the discussion.

In the case when all individuals have a constant length of infection ω, $P(t)$ is a step function with $P(t) = 1$ on $[0, \omega]$ and 0 on (ω, ∞). For consistency the initial infectives must have recovered by time ω, so that $i_0(t) = 0$ for $t \geqq \omega$. In this case the i integral equation in (22) for $t \geqq \omega$ becomes

$$i(t) = \int_{t-\omega}^t \lambda [1 - i(u)]\, i(u) \exp\left[-\int_u^t [\varepsilon(1 - i(p)) + B(N(p)]\, dp \right] du, \tag{24}$$

which is equivalent to the delay-integro-differential equation

$$\begin{aligned} i'(t) = {} & \lambda [1 - i(t)]\, i(t) - \lambda [1 - i(t - \omega)]\, i(t - \omega) \\ & \times \exp\left[-\int_{t-\omega}^t [\varepsilon(1 - i(p)) + B(N(p)]\, dp \right] \\ & - [\varepsilon(1 - i(t)) + B(N(t))]\, i(t). \end{aligned} \tag{25}$$

These equations apply only for $t \geqq \omega$; on the interval $[0, \omega)$, the integral equation is given in (22). Here we find the thresholds and the equilibria, and analyze their stability for this step function case.

7. The thresholds for model 2

In the absence of disease, the population size approaches its carrying capacity K if $N(0) > 0$. But if disease is present, then the population size can go to zero, approach an equilibrium size below the carrying capacity, or approach the carrying capacity, and the disease can die out or persist (remain endemic) depending on the values of some threshold quantities.

The survival probability in the integral equation (18) is

$$Q(t) = P(t) \exp\left[-\int_0^t [\varepsilon + D(N(p))]\, dp \right],$$

so that for the step function $P(t)$, the mean passage time or expected time in the I class during one passage when N is fixed is

$$\int_0^\infty t(-Q'(t))\, dt = \int_0^\infty Q(t)\, dt = \frac{1 - e^{-(\varepsilon + D(N))\omega}}{\varepsilon + D(N)}. \tag{26}$$

Recall that the basic reproduction number is the average number of new cases in the limiting situation when everyone is susceptible. As before the basic reproduction number R_0 is the product of the contact rate λ and the expected time in the infectious class, so the basic reproduction number as a function of N is

$$R_{0N} = \lambda \frac{1 - e^{-(\varepsilon + D(N))\omega}}{\varepsilon + D(N)}. \tag{27}$$

The mean passage in the infective fraction class i is similar with $D(N)$ replaced by $B(N)$, so we define another related threshold quantity called the modified basic reproduction number

$$\tilde{R}_{0N} = \lambda \frac{1 - e^{-(\varepsilon + B(N))\omega}}{\varepsilon + B(N)}. \tag{28}$$

Because $d\tilde{R}_{0N}/dN \gtreqless 0$, $\tilde{R}_{0N}$ is a non-decreasing function of N. The quantities $\tilde{R}_{00}$ and $\tilde{R}_{0K} = R_{0K}$ are two of the thresholds for this model. The threshold $\tilde{R}_{0K}$ determines whether the disease persists or fades out. The threshold $\tilde{R}_{00}$ determines if an equilibrium exists corresponding to disease persistence and population extinction.

When $\varepsilon > 0$, another threshold quantity is given by

$$\psi_0 = \frac{B(0) - D(0)}{\varepsilon} + \frac{1}{R_{00}}. \tag{29}$$

When the disease persists, the parameter ψ_0 determines whether the population persists or approaches extinction due to the disease-related

deaths. Note that $\psi_0 \leqq 1$ implies that $\tilde{R}_{00} \geqq 1$. In the differential equation (21) for N, $B(0) - D(0)$ is the limiting net growth rate function when the population is near extinction and ε is the disease-related death rate constant. Thus the first term in ψ_0 is larger when the net growth function dominates and is smaller when the disease-related loss dominates. The second term is the reciprocal of the basic reproduction number in the limit when the population approaches extinction. The ψ_0 above is the direct analogue of the threshold ψ_0 in [16]. A different threshold quantity ϕ is used in [8], but this threshold is equivalent since $\phi \leqq 1$ is related to a rearrangement of $\psi_0 \leqq 1$.

8. The four equilibria for model 2

In the region U_K of iN space defined by (23), four equilibria are found as fixed points of the equations (21) and (24). Thus $N = 0$ or $\varepsilon i = (B(N) - D(N))$, and $i = 0$ or $1 = \lambda s[1 - \exp(-(\varepsilon s + B(N))\omega]/(\varepsilon s + B(N))$. These equations always have the equilibria $P_1 = (0, 0)$ and $P_2 = (0, K)$ in U_K, which correspond to the fade-out of the disease with the population size at zero or at the carrying capacity K. With $N = 0$ there is another distinct equilibrium solution $i_3 = 1 - s_3$ if

$$F(s_3) = 1 - \frac{\lambda s_3}{\varepsilon s_3 + B(0)}[1 - e^{-(\varepsilon s_3 + B(0))\omega}] = 0. \tag{30}$$

This function satisfies $F(0) = 1$, $F(1) = 1 - \tilde{R}_{00}$, and $F'(s) < 0$, so that $F(s)$ is decreasing on $[0, 1]$. Thus there is a unique equilibrium with $0 < s_3 < 1$ and $i_3 > 0$ iff $\tilde{R}_{00} > 1$. Hence there is a nontrivial equilibrium $P_3 = (i_3, 0)$ in U_K iff the modified basic reproduction number given by (28) satisfies $\tilde{R}_{00} > 1$. Recall that $\psi_0 \leqq 1$ implies that $\tilde{R}_{00} \geqq 1$. The equilibrium P_3 corresponds to persistence of the disease as the population size approaches extinction. Thus the number of infectives is approaching zero, but the infective fraction is approaching i_3, which is positive. Note that $P_3 \to P_1$ as $\tilde{R}_{00} \to 1^+$.

For $\varepsilon > 0$ nonzero i and N values at an equilibrium in U_K must satisfy the two equations

$$\begin{aligned} s &= 1 - i = 1 - [B(N) - D(N)]/\varepsilon = f(N), \\ 1 &- \lambda s \frac{[1 - e^{-(\varepsilon s + B(N))\omega}]}{\varepsilon s + B(N)} = 0. \end{aligned} \tag{31}$$

Note that $f(N)$ is strictly increasing and is positive iff $\varepsilon > B(N) - D(N)$. Moreover, $s = f(N)$ implies $\varepsilon s + B(N) = \varepsilon + D(N)$; substitution of this

into the numerator of the second equation above yields

$$s = \frac{B(N)}{\lambda[1 - e^{-(\varepsilon + D(N))\omega}] - \varepsilon} = g(N). \tag{32}$$

Using methods analogous to those in [16], the fourth equilibrium is shown to exist geometrically by determining when f and g intersect with s in $(0, 1)$ and N in $(0, K)$. The lemma below is useful in the analysis.

Lemma 6. *$\psi_0 \leqq 1$ iff $f(0) \geqq g(0)$ and $\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon > 0$.*

Proof. If $\psi_0 \leqq 1$, then $\varepsilon \geqq B(0) - D(0)$ and

$$\frac{\varepsilon}{\varepsilon - B(0) + D(0)} \leqq R_{00} = \frac{\lambda[1 - e^{-(\varepsilon + D(0))\omega}]}{\varepsilon + D(0)},$$

$$\varepsilon B(0) \leqq \{\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon\}[\varepsilon - B(0) + D(0)],$$

so that $\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon > 0$ and

$$g(0) = \frac{B(0)}{\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon} \leqq \frac{\varepsilon - B(0) + D(0)}{\varepsilon} = f(0).$$

The proof of the opposite implication involves following the rearrangements above in the reverse order. □

First consider the case when $R_{0K} = \tilde{R}_{0K} \leqq 1$, so that

$$\lambda[1 - e^{-(\varepsilon + D(N))\omega}] - \varepsilon \leqq \lambda[1 - e^{-(\varepsilon + D(K))\omega}] - \varepsilon$$
$$\leqq D(K) = B(K) \leqq B(N).$$

If the left side of this inequality is non-positive at some value of N, then $s = g(N)$ is non-positive, so there is no solution s in $(0, 1)$. If the left side of this inequality is positive at some value of N, then the inequality above implies that $s = g(N) \geqq 1$, so there is no solution s in $(0, 1)$. In either case, there is no new equilibrium.

Note that $1 = f(K) > g(K)$ when $R_{0K} = \tilde{R}_{0K} > 1$. Two cases are considered. If $\psi_0 \leqq 1$, then $D'(N) \geqq 0$ and Lemma 6 imply that $\lambda[1 - e^{-(\varepsilon + D(N))\omega}] - \varepsilon > 0$ for N in $(0, K)$. Because $B'(N) \leqq 0$ and $D'(N) \geqq 0$, the function $g(N)$ is a continuous, non-increasing function on $(0, K)$. Because $f(0) \geqq g(0)$ and f is strictly increasing, $f(N) > g(N)$ on $(0, K)$, so they do not intersect to give a new equilibrium. If $\psi_0 > 1$, then Lemma 6 implies that either $f(0) < g(0)$ or $\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon \leqq 0$. If $\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon > 0$, then $f(0) < g(0)$ and $\lambda[1 - e^{-(\varepsilon + D(N))\omega}] - \varepsilon > 0$ on $(0, K)$, so that $g(N)$ is a continuous, non-increasing function on $(0, K)$. Because f is less than g at $N = 0$

and greater than g at $N = K$, they intersect to give a new equilibrium $P_4 = (i_4, N_4)$ with $0 < s_4 < 1$ and $0 < N_4 < K$. If $\lambda[1 - e^{-(\varepsilon + D(0))\omega}] - \varepsilon \leqq 0$, then $\lambda[1 - e^{-(\varepsilon + D(N))\omega}] - \varepsilon = 0$ at some point $\hat{N}$ in $[0, K]$, so that $g(N)$ has a vertical asymptote at $N = \hat{N}$. For N in $[0, \hat{N})$, $g(N)$ is negative, so that s is not in $(0, 1)$. In $(\hat{N}, K]$, g decreases from ∞ down to $g(K) < f(K) = 1$, so that f and g intersect to give a new equilibrium $P_4 = (i_4, N_4)$ with $0 < s_4 < 1$ and $0 < N_4 < K$. This equilibrium P_4 corresponds to persistence of the disease with the population size at an equilibrium level N_4 below K. When $R_{0K} = \tilde{R}_{0K} > 1$, $P_4 \to P_2$ as $\tilde{R}_{0K} \to 1^+$ and $P_4 \to P_3$ as $\psi_0 \to 1^+$. The results above are summarized in the theorem below.

Theorem 7. *With the generalized logistic assumptions above, the system* (24) *and* (21) *in iN space has the equilibria* $P_1 = (0, 0)$ *and* $P_2 = (0, K)$. *It also has the extinction equilibrium* $P_3 = (i_3, 0)$ *iff* $\tilde{R}_{00} > 1$, *and the endemic equilibrium* $P_4 = (i_4, N_4)$ *iff* $\tilde{R}_{0K} > 1$ *and* $\psi_0 > 1$.

9. Stability of disease free equilibria P_1, P_2 in model 2

The $i = 0$ side of U_K is positively invariant and the equation (21) becomes $N'(t) = [B(N) - D(N)]N$, so that $N \to K$ as $t \to \infty$. Thus on the $i = 0$ side of U_K, the equilibrium $P_1 = (0, 0)$ is a repeller and the equilibrium $P_2 = (0, K)$ is attractive. The $N = 0$ side of U_K is positively invariant and the integral equation for i when $N = 0$ is equivalent to that in a previous SIS model with exponential population dynamics [11, pp. 181–185]. Linearization around the equilibrium $P_1 = (0, 0)$ yields an uncoupled system with

$$i(t) = \int_{t-\omega}^{t} \lambda i(u)\, e^{-[\varepsilon + B(0)](t-u)}\, du.$$

From the characteristic equation around $i = 0$, the origin is locally attractive in the i direction if $\tilde{R}_{00} < 1$ and is a local repeller if $\tilde{R}_{00} > 1$. Thus P_1 is like an unstable saddle if $\tilde{R}_{00} < 1$ and is like an unstable node if $\tilde{R}_{00} > 1$. We conjecture that all solutions starting on the $N = 0$ side of U_K approach 0 when $\tilde{R}_{00} \leqq 1$, but have only proved this for $\in \omega \leqq \tilde{R}_{00} \leqq 1$ [11, Theorem 4.2].

Linearization around the equilibrium $P_2 = (0, K)$ yields

$$i(t) = \int_{t-\omega}^{t} \lambda i(u)\, e^{-[\varepsilon + B(K)](t-u)}\, du.$$

Again the characteristic equation around $i = 0$ is the same as in Theorem 4.1 in [11], so that the equilibrium $P_2 = (0, K)$ is locally

attractive in the i direction if $\tilde{R}_{0K} < 1$ and is a local repeller if $\tilde{R}_{0K} > 1$. Thus P_2 is a locally stable attractor if $\tilde{R}_{0K} < 1$ and is like an unstable saddle if $\tilde{R}_{0K} > 1$ with the N axis as the stable manifold and a repulsive direction into the region U_K. If $\tilde{R}_{0K} \leqq 1$ we conjecture that the region U_K except the i axis is an asymptotic stability region for the equilibrium $P_2 = (0, K)$; this is proved below for a restricted range of $\tilde{R}_{0K}$.

Theorem 8. *If* $\varepsilon\omega \leqq \tilde{R}_{0K} \leqq 1$, *then the disease free equilibrium* $P_2 = (0, K)$ *is globally asymptotically stable in the region consisting of* U_K *except the i axis.*

Proof. Using $B(N) \geqq B(K)$ for $0 \leqq N \leqq K$, the proof that $i(t) \to 0$ as $t \to \infty$ is exactly the same as the proof of Theorem 4.2 in [11, p. 185]. This implies that (21) is asymptotically equivalent [14, Chap. 6] to (17), so that $N \to K$ as $t \to \infty$. □

10. Stability of the extinction equilibrium P_3 in model 2

Now consider the equilibrium $P_3 = (i_3, 0)$, which is a distinct equilibrium in U_K iff $\tilde{R}_{00} > 1$. Linearization of (21) and (24) around this equilibrium with $i = i_3 + v$ yields the system

$$N'(t) = [B(0) - D(0) - \varepsilon i_3]N,$$

$$v(t) = \int_{t-\omega}^{t} \lambda \exp[-[\varepsilon(1 - i_3) + B(0)](t - u)] \times \left\{ [1 - 2i_3]v(u) + [1 - i_3]i_3 \int_u^t [\varepsilon v(p) - B'(0)N(p)]\, dp \right\} du.$$

To determine local stability, we substitute $N = c_1 e^{zt}$ and $v = c_2 e^{zt}$ to obtain

$$0 = c_1[z - (B(0) - D(0) - \varepsilon i_3)],$$

$$c_2 e^{zt} = \int_{t-\omega}^{t} \lambda e^{-G_3(t-u)} \left\{ [1 - 2i_3]c_2 e^{zu} + [1 - i_3]\, i_3 \times \int_u^t [\varepsilon c_2 e^{zp} - B'(0)\, c_1 e^{zp}]\, dp \right\} du,$$

where $G_3 = [\varepsilon(1 - i_3) + B(0)]$.

If $c_1 \neq 0$, then the sign of $z = B(0) - D(0) - \varepsilon i_3$ determines whether the linearized eigenvector with an N direction component has a positive or negative eigenvalue. The second equation determines the slope

of this eigenvector as long as $B'(0) \neq 0$. If $B'(0) = 0$, then c_2 can be 0 and then the slope of the eigenvector in the N direction is infinite. Since $z = B(0) - D(0) - \varepsilon + \varepsilon s_3$, $z < 0$ iff $s_3 < 1 - [B(0) - D(0)]/\varepsilon$. Because $F(s)$ given by (30) is decreasing, $s_3 < 1 - [B(0) - D(0)]/\varepsilon$ iff

$$0 = F(s_3) > F(1 - [B(0) - D(0)]/\varepsilon) = 1 - R_{00}\{1 - [B(0) - D(0)]/\varepsilon\}.$$

This is equivalent to $\psi_0 < 1$, where ψ_0 is defined in (29). Thus the equilibrium P_3 is locally attractive in the N direction if $\psi_0 < 1$. Similarly, the equilibrium P_3 is a local repeller in the N direction if $\psi_0 > 1$. Hence, when the disease persists, the threshold ψ_0 determines whether the population persists or approaches extinction.

If $c_1 = 0$ and $c_2 \neq 0$, then there is no N direction component and the second equation is a characteristic equation for z, which is equivalent to the characteristic equation (5.3) in [11] for a similar SIS model with exponential population dynamics. For nearly all parameter values, that equation has all roots with negative real parts, so the equilibrium is attractive in the v direction. Thus in most cases the equilibrium P_3 is like a stable node when $\psi_0 \leqq 1$ and is like a saddle when $\psi_0 > 1$. However, for some very special parameter values given in [11], the real parts of the roots change sign, so that there is Hopf bifurcation at P_3 to a periodic solution $i(t)$ of (24) with $N = 0$. These periodic solutions occur in the side of the region U_K where the population size N is zero.

When $\varepsilon = 0$, then $\psi_0 = \infty > 1$, so that $P_3 = (1 - 1/\tilde{R}_{00}, 0)$ is a repeller in the N direction. In this case the characteristic equation has no roots with non-negative real parts by Theorem 5.1 in [11] (in which the typographical error $\theta < 1$ should be corrected to $\theta > 1$). Because it is a local attractor in the i direction, P_3 is like a saddle.

11. Stability of the endemic equilibrium P_4 in model 2

The equilibrium $P_4 = (i_4, N_4)$ exists in U_K iff $\tilde{R}_{0K} > 1$ and $\psi_0 > 1$. Linearization of (21) and (24) around this equilibrium with $N = N_4 + U$ and $i = i_4 + v$ yields the system

$$U'(t) = [B'(N_4) - D'(N_4)]N_4 U - \varepsilon N_4 v,$$

$$v(t) = \int_{t-\omega}^{t} \lambda \exp[-[\varepsilon s_4 + B(N_4)](t-p)] \times \left\{[2s_4 - 1]v(p) + s_4(1 - s_4)\int_p^t [\varepsilon v(q) - B'(N_4)U(q)]\,dq\right\} dp.$$

To determine local stability, we substitute $U = c_1 e^{zt}$ and $v = c_2 e^{zt}$ to obtain

$$0 = c_1\{z - [B'(N_4) - D'(N_4)]\, N_4)\} + c_2 \varepsilon N_4$$

$$0 = c_1(1 - s_4)\,\frac{B'(N_4)}{z}\left[1 - \lambda s_4\,\frac{1 - \mathrm{e}^{-(z+G_4)\omega}}{z + G_4}\right]$$

$$+ c_2\left\{1 - \lambda\left[(2s_4 - 1) - s_4(1 - s_4)\,\frac{\varepsilon}{z}\right]\frac{1 - \mathrm{e}^{-(z+G_4)\omega}}{z + G_4} - (1 - s_4)\,\frac{\varepsilon}{z}\right\},$$

where $G_4 = [\varepsilon s_4 + B(N_4)] = \varepsilon + D(N_4)$, and $1 = \lambda s_4[1 - \mathrm{e}^{-G_4 w}]/G_4$ has been used to simplify. This system has a nontrivial solution iff the determinant is zero, which after cancellation of some terms gives the characteristic equation

$$\begin{aligned} 0 = {} & (z + G_4)\,[z(z - B'N_4 + D'N_4) - \varepsilon(1 - s_4)(z + D'N_4)] \\ & + \lambda(1 - \mathrm{e}^{-(z+G_4)\omega})\,[(1 - 2s_4)\,z(z - B'N_4 + D'N_4) \\ & + \varepsilon s_4(1 - s_4)(z + D'N_4)] \end{aligned} \tag{33}$$

where $D' = D'(N_4)$ and $B' = B'(N_4)$. This characteristic equation is a quasipolynomial with a cubic term plus a quadratic times an exponential. Using a similar approach with $U = c_1$ and $v = c_2$, it can be shown that $z = 0$ is not a characteristic root.

Because the characteristic equation (33) is complicated and difficult to analyze, we consider a special case with a logistic death structure, where $B(N)$ is constant. Then the integral equation (24) for $i(t)$ is independent of N and also $s_4 = s_3$, so $i_3 = i_4$. In this case with $B'(N) = 0$, one root of (33) is $-D'N_4 < 0$ and the other roots satisfy the characteristic equation

$$\begin{aligned} 0 = {} & (z + G_4)\,[z - \varepsilon(1 - s_4)] + \lambda(1 - \mathrm{e}^{-(z+G_4)\omega}) \\ & \times [(1 - 2s_4)\,z + \varepsilon s_4(1 - s_4)]. \end{aligned}$$

This characteristic equation is equivalent to the characteristic equation in the previous section for the stability of $i(t)$ around the equilibrium P_3 and is also equivalent to (5.3) in [11]. This occurs because equations (24) and (25) are independent of N when $B(N)$ is constant.

Periodic solutions in the variable i can occur. In [11] we found that for parameter values such as $s_3 = 0.005$, $\hat{A} = \lambda\omega = 743$, $\hat{B} = B(0)\omega = 0.0128$ and $\hat{E} = \varepsilon\omega = 721$, the real parts of the characteristic roots

change sign, so that there is Hopf bifurcation to a periodic solution $i(t)$ of (24). If only one of the three parameter values above for $\hat{A}$, $\hat{B}$ and $\hat{E}$ is varied, then periodic solutions $i(t)$ of (25) with a logistic death structure are found numerically for $\hat{A}$ in [728, 751] when $\hat{B}$ and $\hat{E}$ are fixed, $\hat{B}$ in [0, 0.0142] when $\hat{A}$ and $\hat{E}$ are fixed, and $\hat{E}$ in [703, 727] when $\hat{A}$ and $\hat{B}$ are fixed. Thus the parameter region where periodic solutions in i occur seems to be quite small. For parameter values in this small region, we find from (29) that $\psi_0 < 1$, so that P_4 is not in U_K and solutions starting in the interior of U_K are attracted to the $N = 0$ face at rates like e^{-710t}. These solutions that spiral very rapidly down onto the periodic solutions on the $N = 0$ face have also been found numerically.

To summarize the logistic death structure case with $\psi_0 \leqq 1$, for most parameter values the solution $(i(t), N(t))$ approaches the extinction equilibrium P_3 on the $N = 0$ face, but for special parameter values, the infectious fraction solutions $i(t)$ can be periodic or approach periodic solutions while $N(t)$ decreases, so that solution paths are attracted to a periodic solution on the $N = 0$ face. When $\psi_0 > 1$, the equilibrium P_3 is like a saddle with the repulsive direction into the region U_K and the equilibrium P_4 in U_K is locally asymptotically stable, so that it is reasonable to conjecture that all solution paths in the interior of U_K go to P_4. In numerical explorations, we have found similar behavior for other choices of $B(N)$ and $D(N)$, but this has not been proved for the general characteristic equation (33) above.

When $\varepsilon = 0$, equation (21) reduces to (17), so that $N \to K$. Then (24) is asymptotically equivalent [13, Corollary 4.4] to the same equation with $B(N)$ replaced by $B(K)$. In this case (24) is equivalent to the integral equation (2.10) in [11] and Theorem 5.1 in [11] implies that $i \to 1 - 1/\tilde{R}_{0K}$ as $t \to \infty$, so that $P_4 = (1 - 1/\tilde{R}_{0K}, K)$ is locally asymptotically stable.

12. Discussion

In the SIS model with an exponential population structure and a delay corresponding to the infectious period, periodic solutions in the infectious fraction occurred by Hopf bifurcation for a small set of parameter values [11]. Here the threshold quantities and the equilibria have been determined for two analogous SIS models with limited growth population structures. Although some of the characteristic equations in these models are quasipolynomials that are more complicated and difficult to analyze than those in previous models, we have obtained some stability results. For the SIS model with generalized logistic dynamics,

we have found that periodic solutions in the infectious fraction can arise by Hopf bifurcation as the population approaches extinction. All of the analogous SIS models without a delay do not have periodic solutions [16]. Thus the delay destabilizes the infectious fraction equilibrium value for the SIS models with exponential and logistic population dynamics, but this does not occur for the model with recruitment-death population dynamics.

The SIS model with a recruitment-death population structure has only one threshold, the basic reproduction number R_0 that determines whether the disease dies out ($R_0 \leqq 1$ case) or approaches a unique, endemic equilibrium ($R_0 > 1$ case). For this model the endemic equilibrium has been shown to be locally asymptotically stable in a large region, in which case periodic solutions do not arise by Hopf bifurcation.

The SIS model with a generalized logistic population structure has two primary threshold quantities and three different "phase portraits." The basic reproduction number threshold $\tilde{R}_{0K} = R_{0K}$ determines whether the disease fades out (i.e. the infective fraction approaches zero) or persists (i.e. the infective fraction remains bounded away from zero by a positive constant). When the disease persists, the threshold ψ_0 determines whether the population persists ($\psi_0 > 1$) or approaches extinction due to disease-related deaths ($\psi_0 \leqq 1$). When $\tilde{R}_{0K} \leqq 1$ and $N(0) > 0$, then the infectious fraction $i(t)$ goes to zero and the population size $N(t)$ goes to the carrying capacity K. When $\tilde{R}_{0K} > 1$, $i(0) > 0$, and $\psi_0 \leqq 1$, the population size $N(t) \to 0$ as $t \to \infty$. In this case, the persistence of the disease and the disease-related deaths cause the population to approach extinction. Usually the infectious fraction $i(t) \to i_3 > 0$, but for special parameter choices, $i(t)$ can oscillate periodically and approach a periodic solution in the $N = 0$ side of U_K. When $\tilde{R}_{0K} > 1$, $i(0) > 0$, $N(0) > 0$, and $\psi_0 > 1$, then the equilibrium $P_4 = (i_4, N_4)$ is locally asymptotically stable for the logistic deaths population dynamics. In this case, the disease persists and the disease-related deaths cause the population to approach a positive level N_4 below the carrying capacity K. We conjecture that this behavior also occurs for other population dynamics structures and this is supported by numerical simulations.

If the disease-related death coefficient ε is zero in the SIS models, then the population size $N(t)$ approaches the constant size A/d in the first model and the carrying capacity K in the second model as $t \to \infty$. Thus the SIS models here with $\varepsilon = 0$ are asymptotically equivalent to an SIS model with constant population size and a delay corresponding to the infectious period. For such a model the infectious fraction always approaches a constant level [7].

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