SIAM J. APPL. MATH.
Vol. 66, No. 5, pp. 1563–1587

DISCRETE-TIME SIS EPIDEMIC MODEL IN A SEASONAL ENVIRONMENT*

JOHN E. FRANKE† AND ABDUL-AZIZ YAKUBU‡

Abstract. We study the combined effects of seasonal trends and diseases on the extinction and persistence of discretely reproducing populations. We introduce the epidemic threshold parameter, $\mathcal{R}_0$, for predicting disease dynamics in periodic environments. Typically, in periodic environments, $\mathcal{R}_0 > 1$ implies disease persistence on a cyclic attractor, while $\mathcal{R}_0 < 1$ implies disease extinction. We also explore the relationship between the demographic equation and the epidemic process. In particular, we show that in periodic environments, it is possible for the infective population to be on a chaotic attractor while the demographic dynamics is nonchaotic.

Key words. epidemics, infectives, periodic environments, susceptibles

AMS subject classifications. 37G15, 37G35, 39A11, 92B05

DOI. 10.1137/050638345

1. Introduction.

The complexities of a periodic environment can significantly affect the regulation of species [26]. In periodic environments, population sizes are often either enhanced via *resonance* or diminished via *attenuance* [5, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 23, 24, 25, 30, 31, 32, 33, 34, 35, 37, 38, 45, 48, 50]. However, most epidemic models in the literature (with a few exceptions) neglect seasonal factors [3, 4, 12]. For example, Allen and Burgin [1], Allen [2], and Castillo-Chavez and Yakubu [7, 8, 9] studied disease invasions in discretely reproducing populations that live on attractors in constant (nonperiodic) environments. Cushing and Henson [14], Elaydi and Sacker [17, 18, 19, 20], Franke and Yakubu [23, 24], Kocic [35], Kocic and Ladas [36], Kon [37, 38], and others have studied the effects of periodic environments on ecological models without explicit disease dynamics [46].

In this paper, we focus on the impact of seasonal factors on a discrete-time SIS (susceptible-infected-susceptible) epidemic model. The model reduces to the SIS epidemic model of Castillo-Chavez and Yakubu when the environment is constant (nonperiodic) [7, 8, 9]. To understand the impact of seasonality and disease on life-history outcomes, we study the long-term dynamics of our model under specific functional forms for the periodic recruitment function. The periodic Beverton–Holt [6], the periodic constant, and the periodic Malthus (geometric growth) models are the periodic recruitment functions for this study [7, 8, 9].

We assume that a disease invades and subdivides the target population into two classes: susceptibles (noninfectives) and infectives. Prior to the time of disease invasion, the population is assumed to be governed by a periodically forced demographic equation with a periodic recruitment function. Hence, the population is assumed to be either at a demographic "steady state" (an attracting cycle) or growing at a periodic

*Received by the editors August 17, 2005; accepted for publication (in revised form) January 30, 2006; published electronically June 9, 2006. This work was partially supported by funds from the NOAA-NEFSC in Woods Hole, MA.

http://www.siam.org/journals/siap/66-5/63834.html

†Department of Mathematics, North Carolina State University, Raleigh, NC 27695-8205 (franke@math.ncsu.edu).

‡Department of Mathematics, Howard University, Washington, DC 20059 (ayakubu@howard.edu).

geometric rate. The transition from susceptible to infective is a function of the contact rate α (between individuals) and the proportion of infectives (prevalence) in the population. We derive the epidemic threshold parameter, $\mathcal{R}_0$, for predicting disease persistence or extinction in periodic environments. We also explore the relationship between the demographic equation and the epidemic process. Castillo-Chavez and Yakubu, in [7, 8, 9], show that in constant environments the demographic equation drives the disease dynamics. In stark contrast, we use numerical simulations to show that in periodic environments the demographic equation does not always drive the disease dynamics. We show that, in periodic environments, it is possible for the infective population to be on a chaotic attractor while the demographic dynamics is nonchaotic.

The paper is organized as follows. In section 2, we introduce the periodically forced demographic equation for the study. The equation, a nonautonomous nonlinear difference equation with periodic recruitment function, describes the dynamics of the (total) population before disease invasion. We review, in section 2, the results of Franke and Yakubu on periodically forced recruitment functions. The main model, a periodically forced discrete-time SIS epidemic model, is constructed in section 3. When the recruitment function is either a periodic constant or the periodic Beverton–Holt model, then the total population is persistent and lives on a globally attracting cycle. Autonomous discrete-time models do not support (nontrivial) globally stable cycles [21]. In section 4, the basic reproductive number $\mathcal{R}_0$ is introduced and used to predict the (uniform) persistence or extinction of the infective population, where the recruitment function is either a periodic constant or the periodic Beverton–Holt model. Section 5 covers the SIS epidemic model under asymptotically cyclic demographic dynamics, while sections 6 and 7 describe the epidemic model under geometric demographic dynamics. As in section 4, in section 6, $\mathcal{R}_0$ is used to predict the (uniform) persistence or extinction of the proportion of infectives in the total population. Conditions for disease persistence on cyclic attractors are introduced in section 7.

Periodically forced population models support multiple attractors, and we use numerical simulations to show, in section 8, that our periodic epidemic model supports multiple attractors. Section 9 is on period-doubling bifurcations in the epidemic model where the demographic dynamics is simple and nonchaotic. The implications of our results are discussed in section 10.

2. Demographic equations with seasonality. In constant environments, theoretical discrete-time epidemic models are usually formulated under the assumption that the dynamics of the total population size in generation t, denoted by $N(t)$, is governed by equations of the form

$$N(t+1) = f(N(t)) + \gamma N(t), \tag{1}$$

where $\gamma \in (0,1)$ is the constant "probability" of surviving per generation and $f : \mathbb{R}_+ \to \mathbb{R}_+$ models the birth or recruitment process [7, 9].

Seasonality can be introduced into (1) by writing the recruitment function as a p-periodically forced function. This is modeled with the *p-periodic demographic equation*

$$N(t+1) = f(t, N(t)) + \gamma N(t), \tag{2}$$

where $\exists\, p \in \mathbb{N}$ such that

$$f(t, N(t)) = f(t+p, N(t)) \quad \forall t \in \mathbb{Z}_+.$$

We assume throughout that $f(t,N) \in C^2(\mathbb{Z}_+ \times \mathbb{R}_+, \mathbb{R}_+)$ and $\gamma \in (0,1)$ [25].

Franke and Yakubu, in [25], studied model (2) with the periodic constant recruitment function

$$f(t,N(t)) = k_t(1-\gamma)$$

and with the periodic Beverton–Holt recruitment function

$$f(t,N(t)) = \frac{(1-\gamma)\mu k_t N(t)}{(1-\gamma)k_t + (\mu - 1 + \gamma)N(t)},$$

where the carrying capacity k_t is *p-periodic*, $k_{t+p} = k_t$ for all $t \in \mathbb{Z}_+$ [14, 25]. Franke and Yakubu proved that the periodically forced recruitment functions generate globally attracting cycles in model (2) [25]. We summarize their results in the following two theorems.

THEOREM 1. *Model* (2) *with* $f(t,N(t)) = k_t(1-\gamma)$ *has a globally attracting positive s-periodic cycle that starts at*

$$\overline{x}_0 = \frac{(1-\gamma)\left(k_{p-1} + k_{p-2}\gamma + \cdots + k_0\gamma^{p-1}\right)}{1-\gamma^p},$$

where s divides p.

THEOREM 2. *Model* (2) *with* $f(t,N(t)) = \frac{(1-\gamma)\mu k_t N(t)}{(1-\gamma)k_t + (\mu-1+\gamma)N(t)}$ *and* $\mu > 1$ *has a globally attracting positive s-cycle, where s divides p.*

Theorems 1 and 2 imply that the total population is asymptotically periodic (bounded) and lives on a cyclic attractor when the recruitment function is either a periodic constant or the Beverton–Holt model. Denote this cycle by $\{\overline{N}_0, \overline{N}_1, \ldots, \overline{N}_{s-1}\}$. When new recruits arrive at the periodic positive per-capita growth rate λ_t, then

$$f(t,N(t)) = \lambda_t N(t),$$

where $\lambda_{t+p} = \lambda_t$ for all $t \in \mathbb{Z}_+$. The solution to the demographic equation is

$$N(t) = \left(\prod_{J=0}^{t-1} (\lambda_J + \gamma)\right) N(0),$$

and the demographic basic reproductive number is

$$\mathcal{R}_d = \frac{\prod_{J=0}^{p-1} (\lambda_J + \gamma) - \gamma^p}{1-\gamma^p}. \tag{3}$$

$\mathcal{R}_d$ gives the average number of descendants produced by a typically small initial population over a *p-cycle*. If $\mathcal{R}_d < 1$, the total population goes extinct at a geometric rate, and if $\mathcal{R}_d > 1$, the total population explodes at a geometric rate. In constant environments, $p = 1$, $\lambda_J = \lambda$, and $\mathcal{R}_d$ reduces to

$$\mathcal{R}_d = \frac{\lambda}{1-\gamma}.$$

In [7, 8, 9], Castillo-Chavez and Yakubu used $\mathcal{R}_d = \frac{\lambda}{1-\gamma}$ to study the long-term behavior of geometrically growing populations in constant environments.

3. SIS epidemic model in periodic environments. In this section, we introduce the main model, an SIS epidemic model with periodic forcing. To do this, we assume that a nonfatal infectious disease has invaded a population living in a seasonal environment. The population is governed by (2). To model the disease, we build a simple SIS epidemic process on "top" of the periodic demographic equation. We let $S(t)$ denote the population of susceptibles; $I(t)$ denotes the population of the infected, assumed infectious; $N(t) \equiv S(t) + I(t)$ denotes the total population size at generation t, N_∞ denotes the demographic steady state or attracting population, and $\widetilde{N}_0$ the initial point on a globally attracting cycle, when they exist. We assume that individuals survive with constant probability γ each generation, and infected individuals recover with constant probability $(1-\sigma)$.

Let $\phi : [0,\infty) \to [0,1]$ be a monotone concave probability function with $\phi(0) = 1$, $\phi'(x) < 0$, and $\phi''(x) \geq 0$ for all $x \in [0,\infty)$. We assume that the susceptible individuals become infected with nonlinear probability $\left(1 - \phi\left(\alpha \frac{I}{N}\right)\right)$ per generation, where the transmission constant $\alpha > 0$. When infections are modeled as Poisson processes, then $\phi\left(\alpha \frac{I}{N}\right) = e^{-\alpha \frac{I}{N}}$ [7, 8, 9].

Our assumptions and notation lead to the following SIS epidemic model in period p environments:

$$\left.\begin{aligned} S(t+1) &= f(t, N(t)) + \gamma\phi\left(\alpha \tfrac{I(t)}{N(t)}\right) S(t) + \gamma(1-\sigma)I(t), \\ I(t+1) &= \gamma\left(1 - \phi\left(\alpha \tfrac{I(t)}{N(t)}\right)\right) S(t) + \gamma\sigma I(t), \end{aligned}\right\} \tag{4}$$

where $0 < \gamma, \sigma < 1$ and $N(t) > 0$. When the environment is constant, $f(t, N(t)) = f(N(t))$ and model (4) reduces to the model of Castillo-Chavez and Yakubu [7, 8, 9]. The total population in generation $t+1$, $S(t+1) + I(t+1)$, the sum of the two equations of model (4), is the demographic equation (2). Using the substitution $S(t) = N(t) - I(t)$, the I-equation in model (4) becomes

$$I(t+1) = \gamma\left(1 - \phi\left(\alpha \frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) + \gamma\sigma I(t).$$

Let

$$F_N(I) = \gamma\left(1 - \phi\left(\alpha \frac{I}{N}\right)\right)(N - I) + \gamma\sigma I.$$

When F_N has a unique positive fixed point and critical point, we denote them by I_N and C_N, respectively.

$$I(t+1) = F_{N(t)}(I(t)),$$

and the set of iterates of the nonautonomous map $F_{N(t)}$ is the set of density sequences generated by the infective equation. In the next section, we use the map F_N to study disease dynamics in the periodic SIS epidemic model, model (4).

4. Disease extinction versus disease persistence. The classical theory of disease epidemics usually involves computation of an epidemic threshold parameter, the basic reproductive number $\mathcal{R}_0$ [3]. Here, we introduce $\mathcal{R}_0$ and use it to predict the successful invasion or extinction of the disease modeled in (4). In constant environments $f(t, N(t)) = f(N(t))$, and

$$\mathcal{R}_0 = \frac{-\gamma\alpha\phi'(0)}{1 - \gamma\sigma}. \tag{5}$$

$\mathcal{R}_0$ is the average number of secondary infections generated by an initial population of infected (assumed infectious) individuals over their lifetimes [7, 8, 9].

In our periodic model, we use the same $\mathcal{R}_0$ to prove that $\mathcal{R}_0 < 1$ implies disease extinction and $\mathcal{R}_0 > 1$ implies disease persistence. To prove this result we need the following definition [49].

DEFINITION 3. *The total population in model* (2) *is persistent if*

$$\liminf_{t\to\infty} N(t) > 0$$

whenever $N(0) > 0$. *The total population is uniformly persistent if there exists a positive constant* η *such that*

$$\liminf_{t\to\infty} N(t) \geq \eta$$

whenever $N(0) > 0$.

By this definition, when the recruitment function is either a periodic constant or the Beverton–Holt model, the total population is uniformly persistent. Also, when new recruits arrive at the periodic positive per-capita growth rate λ_t and $\mathcal{R}_d > 1$, the total population is uniformly persistent. However, the population goes extinct when $\mathcal{R}_d < 1$.

The following auxiliary lemmas will be used to prove our results.

LEMMA 4. *If* $0 < I(t) \leq N(t)$ *in model* (4), *then* $I(t+1) < \min\{N(t), N(t+1)\}$.

Proof. In model (4),

$$I(t+1) = \gamma\left(1 - \phi\left(\alpha\frac{I(t)}{N(t)}\right)\right)S(t) + \gamma\sigma I(t)$$

and

$$N(t+1) = S(t+1) + I(t+1) = f(t, N(t)) + \gamma N(t).$$

Therefore,

$$\begin{aligned} I(t+1) &= \gamma\left(1 - \phi\left(\alpha\frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) + \gamma\sigma I(t) \\ &< \gamma(N(t) - I(t)) + \gamma I(t) = \gamma N(t) \\ &= N(t+1) - f(t, N(t)) \leq N(t+1). \end{aligned}$$

Hence,

$$I(t+1) < \min\{N(t), N(t+1)\}. \qquad \square$$

LEMMA 5. *If* $I(0) > 0$ *in model* (4), *then* $I(t) > 0$ *for all* $t \in \mathbb{Z}_+$.

Proof. $I(t+1) = \gamma\left(1 - \phi\left(\alpha\frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) + \gamma\sigma I(t)$. By Lemma 4, $N(t) - I(t) \geq 0$ for all $t \in \mathbb{Z}_+$. Therefore, $\gamma\left(1 - \phi\left(\alpha\frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) \geq 0$. $I(0) > 0$ implies $\gamma\sigma I(0) > 0$, and hence $I(1) > 0$. By induction, $I(t) > 0$ and $\gamma\sigma I(t) > 0$. Hence, $I(t+1) > 0$. $\square$

LEMMA 6.

$$F_N(I) = \gamma\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right)(N - I) + \gamma\sigma I$$

satisfies the following conditions:

(a) $F_N'(0) = -\alpha\gamma\phi'(0) + \gamma\sigma$ *and* $F_N'(N) > -1$.
(b) $F_N(I)$ *is concave down on* $[0, N]$.
(c) $F_N(I) \leq F_N'(0)I$ *on* $[0, N]$.
(d) *If* $F_N'(0) > 1$, *then* F_N *has a unique positive fixed point* I_N *in* $[0, N]$.
(e) *Let* $\Psi_N(I) = \frac{I}{N}$. *Then* $F_1(\Psi_N(I)) = \Psi_N(F_N(I))$. *That is,* Ψ_N *is a topological conjugacy between* F_1 *and* F_N.
(f) *If* $N_0 < N_1$ *and* $(-\alpha\gamma\phi'(0) + \gamma\sigma) > 1$, *then* $I_{N_0} < I_{N_1}$ *where* I_{N_i} *is the positive fixed point of* F_{N_i} *in* $[0, N_i]$.
(g) *If* C_1 *exists, then* $C_N = NC_1$.
(h) *If* $N_0 < N_1$, *then* $F_{N_0}(I) < F_{N_1}(I)$ *for all* $I \in (0, N_0]$.

Proof. (a)

$$F_N'(I) = -\frac{\alpha\gamma}{N}\phi'\left(\alpha\frac{I}{N}\right)(N - I) - \gamma\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right) + \gamma\sigma,$$

$$\begin{aligned} F_N'(0) &= -\frac{\alpha\gamma}{N}\phi'(0)(N - 0) - \gamma(1 - \phi(0)) + \gamma\sigma \\ &= -\alpha\gamma\phi'(0) + \gamma\sigma, \end{aligned}$$

$$\begin{aligned} F_N'(N) &= -\frac{\alpha\gamma}{N}\phi'\left(\alpha\frac{N}{N}\right)(N - N) - \gamma\left(1 - \phi\left(\alpha\frac{N}{N}\right)\right) + \gamma\sigma \\ &= -\gamma(1 - \phi(\alpha)) + \gamma\sigma > -\gamma > -1. \end{aligned}$$

(b)

$$F_N''(I) = -\left(\frac{\alpha}{N}\right)^2\gamma\phi''\left(\alpha\frac{I}{N}\right)(N - I) + 2\frac{\alpha\gamma}{N}\phi'\left(\alpha\frac{I}{N}\right).$$

Since $\phi' < 0$ and $\phi'' \geq 0$ on $[0, \infty)$, we have

$$F_N''(I) < 0 \quad \text{on } [0, N].$$

(c) $F_N(0) = 0$ implies that $y = F_N'(0)I$ is the tangent line to the graph of $F_N(I)$ at 0. Since F_N is concave down on $[0, N]$, its graph is below the tangent line at the origin on $[0, N]$. Hence,

$$F_N(I) \leq F_N'(0)I \quad \text{on } [0, N].$$

(d) $F_N(N) = \gamma\sigma N < N$. Since $F_N'(0) > 1$, the graph of $F_N(I)$ starts out higher than the diagonal and must cross it before $I = N$. The concavity property of $F_N(I)$ (see (b)) implies that there is a unique positive fixed point.

(e) $F_1(I) = \gamma(1 - \phi(\alpha I))(1 - I) + \gamma\sigma I$. Thus,

$$F_1(\Psi_N(I)) = \gamma\left(1 - \phi\left(\alpha\frac{I}{N}\right)\right)\left(1 - \frac{I}{N}\right) + \gamma\sigma\frac{I}{N} = \frac{1}{N}F_N(I) = \Psi_N(F_N(I)).$$

(f) Since $F_{N_0}'(0) = (-\alpha\gamma\phi'(0) + \gamma\sigma) > 1$, I_{N_0} exists with $F_{N_0}(I_{N_0}) = I_{N_0}$. Thus $\Psi_{N_0}(F_{N_0}(I_{N_0})) = \Psi_{N_0}(I_{N_0}) = F_1(\Psi_{N_0}(I_{N_0}))$. That is $\Psi_{N_0}(I_{N_0}) = I_1$, the unique positive fixed point of F_1, and $I_{N_0} = N_0 I_1$. Similarly, $I_{N_1} = N_1 I_1$. Hence, $N_0 < N_1$ implies $I_{N_0} < I_{N_1}$.

(g) Topological conjugacy preserves critical points. The result follows from (e).

(h) Let $N_0 < N_1$ and $I \in (0, N_0]$. The topological conjugacy in part (e) shows that $F_{N_0}(I) = N_0 F_1(\frac{I}{N_0})$ and $F_{N_1}(I) = N_1 F_1(\frac{I}{N_1})$. Note that $\frac{I}{N_1} < \frac{I}{N_0}$. Since the graph of F_1 goes through the origin with positive slope and is concave down, the ray through the origin and $\big(\frac{I}{N_1}, F_1(\frac{I}{N_1})\big)$ has a larger slope than the ray through the origin and $\big(\frac{I}{N_0}, F_1(\frac{I}{N_0})\big)$. The first ray contains the point $\big(I, N_1 F_1(\frac{I}{N_1})\big)$, while the second ray contains $\big(I, N_0 F_1(\frac{I}{N_0})\big)$. Hence, $F_{N_1}(I) = N_1 F_1(\frac{I}{N_1}) < N_0 F_1(\frac{I}{N_0}) = F_{N_0}(I)$. □

THEOREM 7. *Let the total population in model* (2) *be uniformly persistent.*

(a) *If* $\mathcal{R}_0 < 1$, *then in model* (4), $\lim_{t\to\infty} I(t) = 0$ *whenever* $I(0) \le N(0)$. *That is, the disease goes extinct.*

(b) *If* $\mathcal{R}_0 > 1$, *then in model* (4), $\exists\ \eta > 0$ *such that* $\lim_{t\to\infty} \inf I(t) \ge \eta$ *whenever* $N(0) \ge I(0) > 0$. *That is, the disease persists uniformly.*

Proof. Since $I(0) \le N(0)$, Lemma 4 implies that $I(t) \le N(t)$ for all $t \in \mathbb{Z}_+$.

(a) $\mathcal{R}_0 = \frac{-\gamma\alpha\phi'(0)}{1-\gamma\sigma} < 1$ is equivalent to $-\alpha\gamma\phi'(0) + \gamma\sigma < 1$. Lemma 6 gives $F'_N(0) = F'_{N(t)}(0) = -\alpha\gamma\phi'(0) + \gamma\sigma < 1$ and $I(t+1) = F_{N(t)}(I(t)) \le F'_{N(t)}(0) I(t)$. Thus, the sequence $\{I(t)\}$ is dominated by the geometrically decreasing sequence $\{(-\alpha\gamma\phi'(0) + \gamma\sigma)^t I(0)\}$, and hence

$$\lim_{t\to\infty} I(t) = 0.$$

(b) Lemma 5 implies that $I(t) > 0$ for all $t \in \mathbb{Z}_+$. Lemma 6 gives $F'_N(0) = F'_{N(t)}(0) = -\alpha\gamma\phi'(0) + \gamma\sigma > 1$. Since $I(t+1) = F_{N(t)}(I(t))$, $I(t+1) > I(t)$ on the open interval $\big(0, I_{N(t)}\big)$. If $I(t) \in (I_{N(t)}, N(t))$, $I(t+1) \ge \min\{I_{N(t)} = N(t)I_1, F_{N(t)}(N(t)) = \gamma\sigma N(t)\}$. Since the total population is uniformly persistent, $\exists\ \widehat{\eta} > 0$ satisfying $\lim_{t\to\infty} \inf N(t) \ge \widehat{\eta}$ whenever $N(0) > 0$. This implies that $\exists\ \eta > 0$ such that

$$\lim_{t\to\infty} \inf \left(\min\{N(t)I_1, \gamma\sigma N(t)\}\right) \ge \eta > 0.$$

Thus, the orbit $\{I(t)\}$ increases when it is small and eventually gets larger and remains larger than a fixed positive number. Hence, $\exists\ \eta > 0$ satisfying

$$\lim_{t\to\infty} \inf I(t) \ge \eta. \qquad \square$$

A slight modification of the proof of Theorem 7 reveals that uniform persistence can be replaced with persistence in the hypothesis and conclusion. That is, if the total population persists, then the disease persists whenever $\mathcal{R}_0 > 1$.

When the recruitment function is either a periodic constant or the periodic Beverton–Holt model, then the (total) population is uniformly persistent. If, in addition, $\mathcal{R}_0 < 1$, then in model (4), $\lim_{t\to\infty} I(t) = 0$, and the disease goes extinct. However, if $\mathcal{R}_0 > 1$, then in model (4), $\lim_{t\to\infty} \inf I(t) \ge \eta > 0$, and the disease persists uniformly (Theorem 7).

In constant environments, when the total population lives on a globally attracting positive fixed point, $\mathcal{R}_0 > 1$ implies uniform persistence of the infectives on a globally attracting positive fixed point [7, 8, 9]. With the advent of periodicity, when the total population lives on an attracting cycle, $\mathcal{R}_0 > 1$ implies uniform persistence of the infectives on a globally attracting cycle (section 5), multiple cyclic attractors (section 8), or a chaotic attractor (section 9). We summarize these results in the following corollary.

COROLLARY 8. *If the demographic equation, model* (2)*, has a globally attracting p-cycle* ($p > 1$) *and* $\mathcal{R}_0 > 1$*, then the uniform persistent infective population in model* (4) *is not on a fixed point attractor.*

Proof. By Theorem 7, the infective population in model (4) is uniformly persistent when $\mathcal{R}_0 > 1$. To establish this result, we use a contradiction proof to show that the infective population in model (4) has no positive fixed point when the demographic equation, model (2), has a globally attracting p-cycle ($p > 1$).

Assume that $(N(0), I(0))$ is an initial condition where $\{I(t)\}$ is constantly fixed at $I(0) > 0$. Now $I(t+1) = F_{N(t)}(I(t)) = I(0)$. Lemma 6 gives the fixed point of $F_{N(t)} = N(t)I_1 = I(0)$. Hence, $\{N(t)\}$ is constantly fixed at $N(0)$. Since all initial total populations are attracted to a nontrivial cycle, we have a contraction. Hence, the uniformly persistent infective population in model (4) is not on a fixed point attractor. □

5. Asymptotically cyclic epidemics. We now study the long-term disease dynamics for a population living in a seasonal environment, where the p-periodic demographic equation has a globally attracting positive cycle $\{\overline{N}_0, \overline{N}_1, \ldots, \overline{N}_{p-1}\}$. For example, when the recruitment function is either periodically constant or periodic Beverton–Holt, the demographic equation is asymptotically cyclic (Theorems 1 and 2). If in addition $\mathcal{R}_0 > 1$, we show that it is possible for the uniformly persistent epidemic to live on a globally attracting cycle. That is, the demographic dynamics drives the disease dynamics. To predict this long-term dynamics of the epidemic process, we use the very general "limiting systems" theory of Franke and Yakubu [23].

The general theory of Franke and Yakubu uses the following periodic hierarchical system:

$$\left.\begin{array}{rcll} x(t+1) & = & g(t,x(t)), & x(0) = x \in R_+^n, \\ y(t+1) & = & h(t,x(t),y(t)), & (x(0),y(0)) = (x,y) \in V \subseteq R_+^{n+m}, \end{array}\right\} \tag{6}$$

where $g : Z_+ \times R_+^n \to R_+^n$ and $h : Z_+ \times V \to R_+^m$ are smooth functions and where there exist smallest positive integers T_1 and T_2 satisfying $g(t+T_1, x(t)) = g(t, x(t))$ and $h(t+T_2, x(t), y(t)) = h(t, x(t), y(t))$, respectively.

Let

$$V = \{(N, I) : I \leq N\}.$$

Then V is a connected set, and for each $N \in \mathbb{R}_+$

$$\{I \in \mathbb{R}_+ : (N, I) \in V\}$$

is a connected set. Lemma 4 shows that the (N, I) system,

$$\left.\begin{array}{l} N(t+1) = f(t, N(t)) + \gamma N(t), \\ I(t+1) = \gamma\left(1 - \phi\left(\alpha \frac{I(t)}{N(t)}\right)\right)(N(t) - I(t)) + \gamma\sigma I(t), \end{array}\right\} \tag{7}$$

is an example of model (6).

System (6) is the sequence of maps $\{G_i\}$, where for each $i \in \mathbb{Z}_+$, $G_i : V \to V$ is defined by

$$G_i(x,y) = (g(i \bmod(T_1), x), h(i \bmod(T_2), x, y)) \equiv (g_i(x), h_i(x,y)).$$

G_i has period $T = \operatorname{lcm}(T_1, T_2)$.

To define a limiting system for system (6), we assume that $\{x_0, x_1, \dots, x_{k-1}\}$ is a *k-cycle* for the T_1-*periodic* dynamical system $\{g_0, g_1, \dots, g_{T_1-1}\}$. For each $i \in \mathbb{Z}_+$, define the sets $V_i = \{y \in \mathbb{R}_+^m : (x_{i \bmod(k)}, y) \in V\}$. Also, define the periodically forced (nonautonomous) maps

$$\widehat{G}_i : \mathbb{R}_+^n \times V_i \to \mathbb{R}_+^n \times V_{i+1} \quad \text{by} \quad \widehat{G}_i(x, y) = (g_i(x), h_i(x_{i \bmod(k)}, y)),$$

and

$$\widehat{H}_i : V_i \to V_{i+1} \quad \text{by} \quad \widehat{H}_i(y) = h_i(x_{i \bmod(k)}, y).$$

Note that

$$\widehat{H}_{kT_2-1} \circ \cdots \circ \widehat{H}_1 \circ \widehat{H}_o : V_0 \to V_0.$$

The periodic system $\{\widehat{G}_0, \widehat{G}_1, \dots, \widehat{G}_{q-1}, \dots\}$ is a limiting system of model (6) when the *k-cycle* is attracting.

Inserting cycle $\{\overline{N}_0, \overline{N}_1, \dots, \overline{N}_{p-1}\}$ into model (7) produces the limiting system

$$\left.\begin{aligned} N(t+1) &= f(t, N(t)) + \gamma N(t), \\ I(t+1) &= \gamma\left(1 - \phi\left(\alpha \tfrac{I(t)}{\overline{N}_t}\right)\right)(\overline{N}_t - I(t)) + \gamma\sigma I(t). \end{aligned}\right\} \tag{8}$$

The second equation of system (8) is $F_{\overline{N}_t}(I(t))$.

The following straightforward generalization of a theorem of Franke and Yakubu gives conditions under which the long-term qualitative dynamics of the nonautonomous system (6) is equivalent to that of the limiting system.

THEOREM 9 (see [23]). *Assume that all orbits of system* (6) *are bounded, V is a connected set, and for each* $x \in \mathbb{R}_+^n$

$$\{y \in \mathbb{R}_+^m : (x, y) \in V\}$$

is a connected set. Then system (6) *has*

$$\{(x_0, y_0), (x_1, y_1), \dots, (x_{l-1}, y_{l-1}), \dots\}$$

as a globally attracting cycle if and only if

$$\{x_0, x_1, \dots, x_{k-1}, \dots\}$$

is a globally attracting k-cycle of the T_1-periodic *dynamical system* $\{g_0, g_1, \dots, g_{T_1-1}\}$ *and* y_0 *is a globally attracting fixed point of the composition* $\widehat{H}_{kT_2-1} \circ \cdots \circ \widehat{H}_1 \circ \widehat{H}_o$.

To apply Theorem 9, we need the following result.

COROLLARY 10. *Assume that all orbits of system* (7) *are bounded. Then system* (7) *has*

$$\{(\overline{N}_0, \overline{I}_0), (\overline{N}_1, \overline{I}_1), \dots, (\overline{N}_{p-1}, \overline{I}_{p-1}), \dots\}$$

as a globally attracting cycle if and only if $\{\overline{N}_0, \overline{N}_1, \dots, \overline{N}_{p-1}, \dots\}$ *is a globally attracting cycle for the p-*periodic *dynamical system* $\{g_0, g_1, \dots, g_{p-1}\}$, *where*

$$g_i(N) = f(i, N) + \gamma N,$$

and $\overline{I}_0$ is a globally attracting fixed point of the composition $\widehat{H}_{p-1} \circ \cdots \circ \widehat{H}_1 \circ \widehat{H}_o$, where

$$\widehat{H}_i(I) = F_{\overline{N}_i}(I) = \gamma\left(1 - \phi\left(\alpha\frac{I}{\overline{N}_i}\right)\right)\left(\overline{N}_i - I\right) + \gamma\sigma I.$$

Now we derive conditions for disease persistence on a globally attracting cycle in periodic environments. In the following result, we prove that the disease lives on a globally attracting cycle when F_1 is a monotone map with no critical points.

THEOREM 11. *If F_1 has no critical points in $[0,1]$ and $\mathcal{R}_0 > 1$, then the composition map*

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point $\overline{I}_0$, and the uniformly persistent epidemic lives on a globally attracting cycle.

Proof. By Lemma 6, each $F_{\overline{N}_i}$ is increasing, concave down, and has no critical point on $[0, \overline{N}_i]$. $\mathcal{R}_0 > 1$ is equivalent to $F'_{\overline{N}_i}(0) > 1$. $F_{\overline{N}_i}(0) = 0$ and $F_{\overline{N}_i}(\overline{N}_i) = \gamma\sigma\overline{N}_i < \overline{N}_i$. Thus, each positive initial condition converges under $F_{\overline{N}_i}$ iterations monotonically to the positive fixed point. That is, $F_{\overline{N}_i}$ has a globally attracting positive fixed point on $[0, \overline{N}_i]$.

By Lemma 4,

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0} : [0, \overline{N}_0] \to [0, \overline{N}_0).$$

Using the chain rule on the composition map $F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$ shows that it is increasing, concave down, and has derivative at the origin larger than 1. So, as in the previous paragraph, $F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$ has a unique globally attracting positive fixed point, $\overline{I}_0$. By Corollary 10, the uniformly persistent epidemic lives on a globally attracting cycle. □

To give a specific example of disease persistence on a globally attracting cycle as predicted by Theorem 11, we assume that infections are modeled as Poisson processes [7, 8, 9]. Then $\phi\left(\alpha\frac{I}{N}\right) = e^{-\alpha\frac{I}{N}}$ and

$$F_{\overline{N}_i}(I) = \gamma\left(1 - e^{-\alpha\frac{I}{\overline{N}_i}}\right)\left(\overline{N}_i - I\right) + \gamma\sigma I. \tag{9}$$

EXAMPLE 12. *In (9), set the following parameter values:*

$$\alpha = 2, \quad \gamma = 0.9, \quad \sigma = .9.$$

From the graph of F_1 (see Figure 1) it is clear that F_1 has no critical points in $[0,1]$ and $\mathcal{R}_0 > 1$.

Hence, with these parameters, the composition map

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point, $\overline{I}_0$, and the uniformly persistent epidemic lives on a globally attracting cycle (Theorem 11). Numerical experiments show that this result is also true when $\alpha \in [1, 2.1]$, $\gamma = [0.88, 1)$, and $\sigma = [0.88, 1)$; as well as on other intervals.

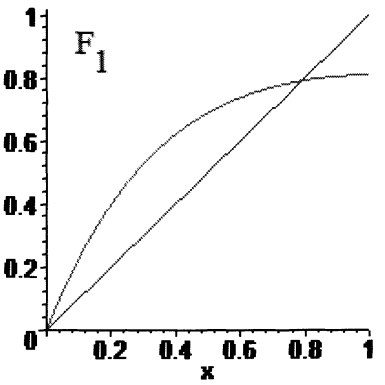

FIG. 1. *Graph of F_1 satisfies the hypotheses of Theorem* 11.

If in Example 12 the recruitment function is the periodic Beverton–Holt model

$$f(t, N(t)) = \frac{(1-\gamma)\mu k_t N(t)}{(1-\gamma)k_t + (\mu - 1 + \gamma)N(t)}$$

with

$$\mu = 2, \quad \gamma = 0.9, \quad \alpha = 2, \quad \sigma = 0.9, \quad p = 2, \quad k_0 = 2, \quad k_1 = 8,$$

then, as predicted by Theorem 11, the total population, susceptible population, and infective population live on the globally attracting 2-cycle

$$\{(8.087, 1.903, 6.184), (7.788, 1.437, 6.351)\}.$$

In the following result, we prove that the disease lives on a globally attracting cycle when F_1 has a critical point with an image (under F_1 iteration) smaller than the critical point.

THEOREM 13. *Let F_1 have a critical point, C_1, in $(0,1)$. If*

$$C_1 > F_1(C_1), \qquad F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) < C_{\min\{\overline{N}_i\}},$$

and $\mathcal{R}_0 > 1$, then the composition map

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point $\overline{I}_0$, and the uniformly persistent epidemic lives on a globally attracting cycle.

Proof. By Lemma 6 and our hypothesis, each $F_{\overline{N}_i}$ is increasing, concave down, and has no critical point on $[0, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$. Since $C_1 > F_1(C_1)$, $I_1 < C_1$ and F_1 is increasing on $[I_1, C_1]$. Consequently, $I_1 < F_1(C_1)$, and by topological conjugacy and Lemma 6, $I_{\overline{N}_i} < F_{\overline{N}_i}(C_{\overline{N}_i}) \le F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) < C_{\min\{\overline{N}_i\}}$. Further, $\mathcal{R}_0 > 1$ is equivalent to $F'_{\overline{N}_i}(0) > 1$. Thus, each positive initial condition converges under $F_{\overline{N}_i}$ iterations monotonically to the positive fixed point. That is, $F_{\overline{N}_i}$ has a globally attracting positive fixed point on $[0, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$.

By the preceding arguments,

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0} : [0, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})] \to [0, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})).$$

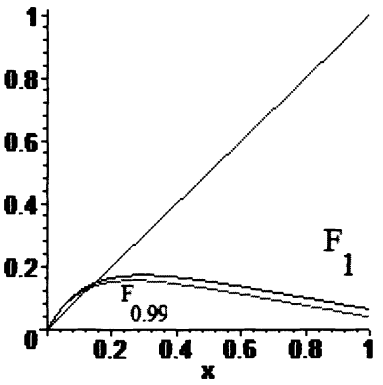

FIG. 2. *Graphs of* F_1 *and* $F_{0.99}$ *satisfy the hypotheses of Theorem* 13.

Using the chain rule on the composition map $F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$ shows that it is increasing, concave down, and has derivative at the origin larger than 1. So, as in the previous paragraph, $F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$ has a unique globally attracting positive fixed point on $[0, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$. Since $F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})$ is the maximum value of all the $F_{\overline{N}_i}$, every point immediately gets into $[0, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$, and the composition map

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point, $\overline{I}_0$. By Corollary 10, the uniformly persistent epidemic lives on a globally attracting cycle. □

Next we demonstrate, via a specific example, disease persistence on a globally attracting cycle, as predicted by Theorem 13.

EXAMPLE 14. *In* (9), *set the following parameter values:*

$$\alpha = 7, \quad \gamma = 0.25, \quad \sigma = 0.25, \quad \max\{\overline{N}_i\} = 1, \quad \min\{\overline{N}_i\} = .99.$$

From the graphs of $F_{\max\{\overline{N}_i\}}$ *and* $F_{\min\{\overline{N}_i\}}$ *(see Figure* 2*) it is clear that* $C_1 > F_1(C_1)$,

$$F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) < C_{\min\{\overline{N}_i\}},$$

and $\mathcal{R}_0 > 1$.

Hence, with these parameters, the composition map

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point $\overline{I}_0$, and the uniformly persistent epidemic lives on a globally attracting cycle. Numerical experiments show that this result is also true when $\alpha \in [7, 10]$, $\gamma = [0.15, 0.25]$, $\sigma = [0.15, 0.25]$, and $\overline{N}_J \in [0.9, 1]$; as well as on other intervals.

If in Example 14 the recruitment function is the periodic Beverton–Holt model

$$f(t, N(t)) = \frac{(1-\gamma)\mu k_t N(t)}{(1-\gamma)k_t + (\mu - 1 + \gamma)N(t)}$$

with

$$\mu = 2, \quad \gamma = 0.25, \quad \alpha = 7, \quad \sigma = 0.25, \quad p = 2, \quad k_0 = 0.665, \quad k_1 = 0.965,$$

then

$$\max\{\overline{N}_i\} = 0.995, \qquad \min\{\overline{N}_i\} = 0.905,$$

and, as predicted by Theorem 13, the total population, susceptible population, and infective population live on the globally attracting 2-cycle

$$\{(0.995, 0.860, 0.135), (0.905, 0.765, 0.140)\}.$$

Next, we prove that the disease lives on a globally attracting cycle when F_1 has a critical point with an image (under F_1 iteration) bigger than the critical point.

THEOREM 15. *Let F_1 have a critical point, C_1, in $(0,1)$. If*

$$C_1 < F_1(C_1), \qquad F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) < \min\{\overline{N}_i\},$$

$$C_{\max\{\overline{N}_i\}} < F_{\min\{\overline{N}_i\}} \circ F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}),$$

and $\mathcal{R}_0 > 1$, then the composition map

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point $\overline{I}_0$, and the uniformly persistent epidemic lives on a globally attracting cycle.

Proof. By Lemma 6 and our hypothesis, each $F_{\overline{N}_i}$ is decreasing on $[C_{\overline{N}_i}, \overline{N}_i] \supseteq [C_{\max\{\overline{N}_i\}}, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$ and $F_{\overline{N}_i}(C_{\max\{\overline{N}_i\}}) \le F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})$. By our hypothesis, $C_{\max\{\overline{N}_i\}} < F_{\min\{\overline{N}_i\}} \circ F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) \le F_{\overline{N}_i} \circ F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})$. Thus, each $F_{\overline{N}_i}$ is decreasing on $[C_{\max\{\overline{N}_i\}}, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$ and sends this interval into itself. Consequently, each $F_{\overline{N}_i}$ has a fixed point $I_{\overline{N}_i}$ in this interval. Since $F'_{\overline{N}_i}(I) \in (-1, 0]$ for all $I \in [C_{\max\{\overline{N}_i\}}, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$ and $\overline{N}_i \in \{\overline{N}_0, \overline{N}_1, \ldots, \overline{N}_{p-1}\}$ (Lemma 6), each $F_{\overline{N}_i}$ is a contraction on this interval. This implies that $F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$ is a contraction with a unique fixed point, which is $\overline{I}_0$.

By Lemma 6 and our hypothesis, $F_{\overline{N}_i}(I) < F_{\overline{N}_i}(C_{\overline{N}_i}) \le F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) < \min\{\overline{N}_i\}$ for all $I \in [0, \overline{N}_i]$ and $\overline{N}_i \in \{\overline{N}_0, \overline{N}_1, \ldots, \overline{N}_{p-1}\}$. $F_{\overline{N}_i}(I) > I$ for all $I \in (0, I_{\overline{N}_i})$. Thus, all positive points below $C_{\max\{\overline{N}_i\}}$ increase until they are in $[C_{\max\{\overline{N}_i\}}, F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}})]$. Consequently, $F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$ has a globally attracting positive fixed point, $\overline{I}_0$, and by Corollary 10, the uniformly persistent epidemic lives on a globally attracting cycle. □

Now we demonstrate, via a specific example, disease persistence on a globally attracting cycle, as predicted by Theorem 15.

EXAMPLE 16. *In (9) set the following parameter values:*

$$\alpha = 20, \quad \gamma = 0.5, \quad \sigma = .5, \quad \max\{\overline{N}_i\} = 1, \quad \min\{\overline{N}_i\} = .7.$$

From the graphs of $F_{\max\{\overline{N}_i\}}$ and $F_{\min\{\overline{N}_i\}}$ (see Figure 3) it is clear that

$$C_1 < F_1(C_1), \qquad F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}) < \min\{\overline{N}_i\},$$

$$C_{\max\{\overline{N}_i\}} < F_{\min\{\overline{N}_i\}} \circ F_{\max\{\overline{N}_i\}}(C_{\max\{\overline{N}_i\}}),$$

and $\mathcal{R}_0 > 1$.

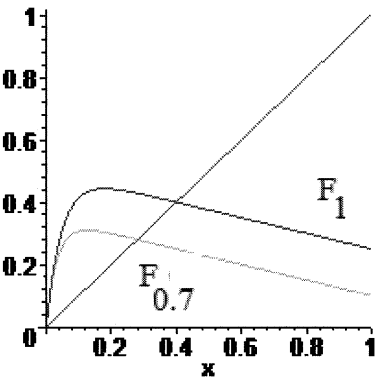

FIG. 3. *Graphs of F_1 and $F_{0.7}$ satisfy the hypotheses of Theorem* 15.

Hence, with these parameters, the composition map

$$F_{\overline{N}_{p-1}} \circ \cdots \circ F_{\overline{N}_1} \circ F_{\overline{N}_0}$$

has a globally attracting positive fixed point $\overline{I}_0$, and the uniformly persistent epidemic lives on a globally attracting cycle. Numerical experiments show that this result is also true when $\alpha \in [15, 25]$, $\gamma = [0.45, 0.6)$, $\sigma = [0.45, 0.6)$, and $\overline{N}_J \in [0.7, 1]$; as well as on other intervals.

If in Example 16 the recruitment function is the periodic Beverton–Holt model

$$f(t, N(t)) = \frac{(1-\gamma)\mu k_t N(t)}{(1-\gamma)k_t + (\mu - 1 + \gamma)N(t)}$$

with

$$\mu = 2, \quad \alpha = 20, \quad \gamma = 0.5, \quad \sigma = .5, \quad p = 2, \quad k_0 = 0.1, \quad k_1 = 0.9,$$

then

$$\max\{\overline{N}_i\} = 0.917, \qquad \min\{\overline{N}_i\} = 0.741,$$

and, as predicted by Theorem 15, the total population, susceptible population, and infective population live on the globally attracting 2-cycle

$$\{(0.917, 0.644, 0.273), (0.741, 0.352, 0.389)\}.$$

In all the above examples, we use the periodic Beverton–Holt model as the recruitment function to highlight uniform persistence via attracting cycles. Similar examples can be obtained using the periodic constant recruitment function.

6. Uniform persistence and geometric demographics. When new recruits arrive at the periodic positive per-capita growth rate λ_t, the demographic long-term dynamics is determined by the demographic basic reproductive number $\mathcal{R}_d$ (see (3)). In this case, we use proportions to study the epidemic process. We introduce the new variables

$$s(t) = \frac{S(t)}{N(t)}$$

and

$$i(t) = \frac{I(t)}{N(t)}.$$

In the new variables, when $f(t, N) = \lambda_t N$, then

$$N(t+1) = (\lambda_t + \gamma)\, N(t),$$

and model (4) becomes

$$\left.\begin{aligned} s(t+1) &= \tfrac{\lambda_t}{\lambda_t+\gamma} + \tfrac{\gamma\phi(\alpha i(t))}{\lambda_t+\gamma} s(t) + \tfrac{\gamma(1-\sigma)}{\lambda_t+\gamma} i(t), \\ i(t+1) &= \tfrac{\gamma(1-\phi(\alpha i(t)))}{\lambda_t+\gamma} s(t) + \tfrac{\gamma\sigma}{\lambda_t+\gamma} i(t). \end{aligned}\right\} \tag{10}$$

Since $i(t)+s(t) = 1$ for all t, the substitution $s(t) = 1-i(t)$ reduces the i-equation of the system to the one-dimensional nonautonomous equation

$$i(t+1) = \frac{\gamma\,(1-\phi\,(\alpha i(t)))}{\lambda_t+\gamma}\,(1-i(t)) + \frac{\gamma\sigma}{\lambda_t+\gamma} i(t).$$

Let

$$\widetilde{F}_\lambda(i) = \frac{\gamma\,(1-\phi\,(\alpha i))}{\lambda+\gamma}\,(1-i) + \frac{\gamma\sigma}{\lambda+\gamma} i.$$

Since $i \le 1$,

$$\widetilde{F}_\lambda(i) < 1 \quad \text{and} \quad \widetilde{F}_\lambda(i) = \frac{1}{\lambda+\gamma} F_1(i).$$

By Lemma 6,

$$\widetilde{F}'_\lambda(0) = \frac{-\alpha\gamma\phi'\,(0) + \gamma\sigma}{\lambda+\gamma}$$

and

$$\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) = \frac{(-\alpha\gamma\phi'\,(0) + \gamma\sigma)^p}{\prod_{t=0}^{p-1}(\lambda_t+\gamma)}.$$

Let

$$\mathcal{R}_0 = \frac{-\alpha\gamma\phi'\,(0)}{(\mathcal{R}_d(1-\gamma^p)+\gamma^p)^{\frac{1}{p}} - \gamma\sigma}.$$

If $\mathcal{R}_d = 1$, the total population is bounded and uniformly persistent, and $\mathcal{R}_0$ reduces to $\frac{-\alpha\gamma\phi'(0)}{1-\gamma\sigma}$, which is (5). We will prove that $\mathcal{R}_0 > 1$ implies that $i(t)$ persists, and $\mathcal{R}_0 < 1$ implies $\lim_{t\to\infty} i(t) = 0$. First, we obtain local stability results when $\mathcal{R}_0 \neq 1$.

LEMMA 17. *$\mathcal{R}_0 > 1$ is equivalent to $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) > 1$, and $\mathcal{R}_0 < 1$ is equivalent to $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) < 1$.*

Proof. Assume $\mathcal{R}_0 > 1$; then

$$\frac{-\alpha\gamma\phi'\,(0)}{(\mathcal{R}_d(1-\gamma^p)+\gamma^p)^{\frac{1}{p}} - \gamma\sigma} > 1.$$

Since $-\alpha\gamma\phi'(0) > 0$, $(\mathcal{R}_d(1-\gamma^p)+\gamma^p)^{\frac{1}{p}} - \gamma\sigma > 0$ and $-\alpha\gamma\phi'(0) > (\mathcal{R}_d(1-\gamma^p)+\gamma^p)^{\frac{1}{p}} - \gamma\sigma$. This implies that

$$(-\alpha\gamma\phi'(0)+\gamma\sigma)^p > \mathcal{R}_d(1-\gamma^p)+\gamma^p = \frac{\prod_{J=0}^{p-1}(\lambda_J+\gamma)-\gamma^p}{1-\gamma^p}(1-\gamma^p)+\gamma^p$$
$$= \prod_{J=0}^{p-1}(\lambda_J+\gamma).$$

Hence,

$$\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) = \frac{(-\alpha\gamma\phi'(0)+\gamma\sigma)^p}{\prod_{J=0}^{p-1}(\lambda_J+\gamma)} > 1.$$

Since all the steps are reversible, $\mathcal{R}_0 > 1$ is equivalent to $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) > 1$.

To prove the other inequality, note that $(\mathcal{R}_d(1-\gamma^p)+\gamma^p)^{\frac{1}{p}} - \gamma\sigma > (\gamma^p)^{\frac{1}{p}} - \gamma\sigma > 0$, and proceed as in the proof of the last inequality. □

THEOREM 18. *Let*

$$f(t,N) = \lambda_t N$$

in model (2), *where* $\lambda_{t+p} = \lambda_t$.

(a) *If* $\mathcal{R}_0 < 1$, *then in model* (10), $\lim_{t\to\infty} i(t) = 0$. *That is, the proportion of infectives in the total population goes extinct.*

(b) *If* $\mathcal{R}_0 > 1$, *then in model* (10), $\exists\ \eta > 0$ *satisfying* $\lim_{t\to\infty} \inf i(t) \geq \eta$. *That is, the proportion of infectives in the total population uniformly persists.*

Proof. (a) Lemma 17 shows that $\mathcal{R}_0 < 1$ implies

$$\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) = \frac{(-\alpha\gamma\phi'(0)+\gamma\sigma)^p}{\prod_{J=0}^{p-1}(\lambda_J+\gamma)} < 1.$$

Let $i > 0$; then $\widetilde{F}_\lambda(i) = \frac{1}{\lambda+\gamma}F_1(i) < \frac{1}{\lambda+\gamma}F_1'(0)i = \frac{-\alpha\gamma\phi'(0)+\gamma\sigma}{\lambda+\gamma}i$, by Lemma 6. Using this p times gives

$$i(p) = \left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)(i(0)) < \frac{(-\alpha\gamma\phi'(0)+\gamma\sigma)^p}{\prod_{J=0}^{p-1}(\lambda_J+\gamma)}i(0) < i(0).$$

Thus, the sequence $\{i(tp)\}$ is dominated by the geometrically decreasing sequence

$$\left\{\left(\frac{(-\alpha\gamma\phi'(0)+\gamma\sigma)^p}{\prod_{J=0}^{p-1}(\lambda_J+\gamma)}\right)^t i(0)\right\}$$

and hence, by continuity of the system,

$$\lim_{t\to\infty} i(t) = 0.$$

(b) Lemma 17 shows that $\mathcal{R}_0 > 1$ implies

$$\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) > 1.$$

Since $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)(0) = 0$, the graph of $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ starts out above the diagonal. Since for each λ_J and each $i \in [0,1]$, $\widetilde{F}_{\lambda_J}(i) < 1$, $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)(1) < 1$. Thus $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has at least one positive fixed point. Let i^* be the minimum of these positive fixed points; then $i((t+1)p) > i(tp)$ when $i(tp)$ is in the open interval $(0, i^*)$.

Let

$$m = \min\left\{\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)(i) : i \in [i^*, 1]\right\}.$$

Note that $m > 0$. If $i(tp) \in (0, m)$, then $i((t+1)p) > i(tp)$, and the sequence $\{i(tp)\}$ continues to increase until the value is at least m. But then the sequence can never jump lower than m. Hence,

$$\lim_{t\to\infty} \inf i(tp) \geq m.$$

Now each of the maps $\widetilde{F}_{\lambda_0}, \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}, \ldots, \widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has positive minima on $[m, 1]$, and $\lim_{t\to\infty} \inf i(t)$ is at least the minimum of these minima. Hence, $\exists\ \eta > 0$ satisfying

$$\lim_{t\to\infty} \inf i(t) > \eta. \qquad \square$$

7. Cyclic attractors and geometric demographics. We assume that the total population is growing geometrically. That is, the recruitment function in the p-periodic demographic equation is $f(t, N(t)) = \lambda_t N(t)$. If, in addition,

$$\mathcal{R}_0 = \frac{-\alpha\gamma\phi'(0)}{\left(\mathcal{R}_d(1-\gamma^p) + \gamma^p\right)^{\frac{1}{p}} - \gamma\sigma} > 1,$$

we show that it is possible for the persistent i-population to live on a globally attracting cycle. This implies that both the *i-dynamics* under periodic geometric recruitment function and the *I-dynamics* under either periodic constant or periodic Beverton–Holt recruitment functions are capable of living on globally attracting cycles.

Next, we prove that the proportion of infectives live on a globally attracting cycle when $\widetilde{F}_{\lambda_t}$ is a monotone map with no critical points.

THEOREM 19. *If each $\widetilde{F}_{\lambda_t}$ has no critical points in $[0,1]$ and $\mathcal{R}_0 > 1$, then the composition map*

$$\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$$

has a globally attracting positive fixed point $\bar{i}_0$, and the uniformly persistent proportion of infectives in the total population lives on a globally attracting cycle.

Proof. By Lemma 6 each $\widetilde{F}_{\lambda_t}(i) = \frac{1}{\lambda_t+\gamma} F_1(i)$ is increasing, concave down, and has no critical point on $[0,1]$. Hence, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ is also increasing, concave down, and has no critical point on $[0,1]$. $\mathcal{R}_0 > 1$ is equivalent to $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) > 1$. Since

$$\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)(0) = 0,$$

$\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has a fixed point in $(0,1)$. Thus, each positive initial condition converges monotonically under iteration of $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ to the positive fixed

point. That is, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has a globally attracting positive fixed point on $[0,1]$, and the uniformly persistent proportion of infectives in the total population lives on a globally attracting cycle. □

To give a specific example of disease persistence on a globally attracting cycle as predicted by Theorem 19, following Example 12, we assume that infections are modeled as Poisson processes [7, 8, 9]. Then $\phi(\alpha i) = e^{-\alpha i}$, $\phi'(0) = -1$, and

$$\widetilde{F}_\lambda(i) = \frac{\gamma\left(1 - e^{-\alpha i}\right)}{\lambda + \gamma}(1 - i) + \frac{\gamma\sigma}{\lambda + \gamma} i. \tag{11}$$

EXAMPLE 20. *In* (11), *set the following parameters:*

$$\alpha = 2, \quad \gamma = 0.9, \quad \sigma = 0.9, \quad \lambda_0, \lambda_1 \in [0.1, 0.75].$$

As in Example 12, $\widetilde{F}_\lambda$ has no critical point in $[0,1]$. For the special case $\alpha = 2$, $\gamma = 0.9$, $\sigma = 0.9$, $\lambda_0 = 0.5$, and $\lambda_1 = 0.6$ the proportion of infectives in the total population lives on the stable period 2 orbit $\{0.447, 0.469\}$ (see Theorem 19).

Now, we prove that the disease lives on a globally attracting cycle when F_1 has a critical point with an image (under $\widetilde{F}_{\max\{\lambda_t\}}$ iteration) smaller than the critical point.

THEOREM 21. *Let each F_λ have a critical point, C_1, in $(0,1)$. If*

$$\widetilde{F}_{\min\{\lambda_t\}}(C_1) < C_1$$

and $\mathcal{R}_0 > 1$, then the composition map

$$\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$$

has a globally attracting positive fixed point $\bar{i}_0$, and the uniformly persistent proportion of infectives in the total population lives on a globally attracting cycle.

Proof. By Lemma 6 and our hypothesis, each $\widetilde{F}_{\lambda_t}(i) = \frac{1}{\lambda_t + \gamma} F_1(i)$ has C_1 as its only critical point on $[0,1]$, is increasing on $[0, C_1]$, and concave down on $[0,1]$. We also have

$$\widetilde{F}_{\max\{\lambda_t\}}(i) \le \widetilde{F}_{\lambda_t}(i) \le \widetilde{F}_{\min\{\lambda_t\}}(i).$$

Since $\widetilde{F}_{\min\{\lambda_t\}}(C_1) < C_1$, the image of each $\widetilde{F}_{\lambda_t}$ is in $[0, C_1)$. Thus, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has C_1 as its only critical point, and its image is in $[0, C_1)$. Hence, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ is increasing and concave down on $[0, C_1]$.

$\mathcal{R}_0 > 1$ is equivalent to $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) > 1$. Since $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)(0) = 0$, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has a fixed point in $(0, C_1)$. Thus, each positive initial condition gets into $[0, C_1]$ and converges monotonically under iteration of $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ to the positive fixed point. That is, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has a globally attracting positive fixed point on $(0,1]$, and the uniformly persistent proportion of infectives in the total population lives on a globally attracting cycle. □

To give a specific example of disease persistence on a globally attracting cycle as predicted by Theorem 21, following Example 14, we assume that infections are modeled as Poisson processes [7, 8, 9].

EXAMPLE 22. *In* (11), *set the following parameter values:*

$$\alpha \in [7, 10], \quad \gamma \in [0.15, 0.25], \quad \sigma \in [0.15, 0.25], \quad \lambda_0, \lambda_1 \in [0.85, 1.0].$$

As in Example 14, all the conditions of Theorem 21 are satisfied. For the special case $\alpha = 7$, $\gamma = 0.25$, $\sigma = 0.25$, $\lambda_0 = 0.85$, and $\lambda_1 = 0.95$ the proportion of infectives in the total population lives on the stable period 2 orbit $\{0.107, 0.113\}$ (see Theorem 21).

Next, we prove that the disease lives on a globally attracting cycle when F_1 has a critical point with an image (under $\widetilde{F}_{\max\{\lambda_t\}}$ iteration) bigger than the critical point.

THEOREM 23. *Let F_1 have a critical point, C_1, in $(0,1)$. If*

$$C_1 < \widetilde{F}_{\max\{\lambda_t\}} \circ \widetilde{F}_{\min\{\lambda_t\}}(C_1),$$

then $\mathcal{R}_0 > 1$, and the composition map

$$\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$$

has a globally attracting positive fixed point $\bar{i}_0$, and the uniformly persistent proportion of infectives in the total population lives on a globally attracting cycle.

Proof. By Lemma 6 and our hypothesis, each $\widetilde{F}_{\lambda_t}(i) = \frac{1}{\lambda_t+\gamma}F_1(i)$ has C_1 as its only critical point on $[0,1]$, is increasing on $[0, C_1]$, and concave down on $[0,1]$. We also have

$$\widetilde{F}_{\max\{\lambda_t\}}(i) \le \widetilde{F}_{\lambda_t}(i) \le \widetilde{F}_{\min\{\lambda_t\}}(i).$$

Since $C_1 < \widetilde{F}_{\max\{\lambda_t\}} \circ \widetilde{F}_{\min\{\lambda_t\}}(C_1) < \widetilde{F}_{\max\{\lambda_t\}}(C_1) \le \widetilde{F}_{\lambda_t}(C_1)$ and $\widetilde{F}_{\lambda_t}(0) = 0$, each $\widetilde{F}'_{\lambda_t}(0) > 1$. Hence, $\left(\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}\right)'(0) > 1$ and, by Lemma 17, $\mathcal{R}_0 > 1$.

By our hypothesis, $C_1 < \widetilde{F}_{\max\{\lambda_t\}} \circ \widetilde{F}_{\min\{\lambda_t\}}(C_1) \le \widetilde{F}_{\lambda_t} \circ \widetilde{F}_{\min\{\lambda_t\}}(C_1)$ and $\widetilde{F}_{\lambda_t}(C_1) \le \widetilde{F}_{\min\{\lambda_t\}}(C_1)$ for each λ_t. Thus, each $\widetilde{F}_{\lambda_t}$ is decreasing on $[C_1, \widetilde{F}_{\min\{\lambda_t\}}(C_1)]$ and sends this interval into itself. Consequently, each $\widetilde{F}_{\lambda_t}$ has a fixed point $\bar{i}_{\lambda_t}$ in this interval:

$$\begin{aligned}\widetilde{F}'_{\lambda_i}(i) &= \frac{1}{\lambda_i+\gamma}F'_1(i) = \frac{1}{\lambda_i+\gamma}\left(-\alpha\gamma\phi'(\alpha i)(1-i) - \gamma(1-\phi(\alpha i)) + \gamma\sigma\right)\\ &> \frac{-\gamma}{\lambda_i+\gamma} > -1.\end{aligned}$$

Hence, $\widetilde{F}'_{\lambda_i}(i) \in (-1, 0]$ for all $i \in [C_1, \widetilde{F}_{\min\{\lambda_t\}}(C_1)]$ and all λ_i. Each $\widetilde{F}_{\lambda_i}$ is a contraction on this interval. This implies that $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ is a contraction with a unique fixed point in $[C_1, \widetilde{F}_{\min\{\lambda_t\}}(C_1)]$. Thus, all positive points below C_1 increase until they are in $[C_1, \widetilde{F}_{\min\{\lambda_t\}}(C_1)]$. Consequently, $\widetilde{F}_{\lambda_{p-1}} \circ \cdots \circ \widetilde{F}_{\lambda_1} \circ \widetilde{F}_{\lambda_0}$ has a globally attracting positive fixed point on $(0,1]$, and the uniformly persistent proportion of infectives in the total population lives on a globally attracting cycle. □

To give a specific example of disease persistence on a globally attracting cycle as predicted by Theorem 23, following Example 16, we assume that infections are modeled as Poisson processes [7, 8, 9].

EXAMPLE 24. *In (11), set the following parameter values:*

$$\alpha \in [15, 25], \quad \gamma \in [0.45, 0.6], \quad \sigma \in [0.45, 0.6], \quad \lambda_0, \lambda_1 \in [0.7, 1.0].$$

As in Example 16, all the conditions of Theorem 23 are satisfied. For the special case $\alpha = 20$, $\gamma = 0.5$, $\sigma = 0.5$, $\lambda_0 = 0.8$, and $\lambda_1 = 0.9$ the proportion of infectives in the total population lives on the stable period 2 orbit $\{0.289, 0.327\}$ (see Theorem 23).

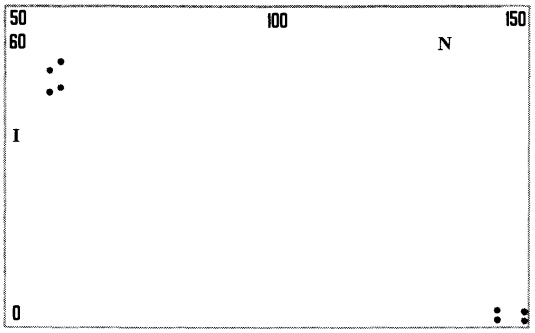

FIG. 4. *Two attracting 4-cycles (multiple attractors). Red and black attractors.*

8. Multiple attractors. In constant environments, single patch discrete-time epidemic models typically support only one attractor [7, 8, 9]. Henson and coworkers [30, 31, 32, 33], Franke and Selgrade [22], and Franke and Yakubu [24] found multiple attractors in periodically forced models, where the corresponding models in constant environments have no multiple attractors. These multiple attractors are a result of periodic perturbations of the corresponding models in constant environments. In this section, we illustrate that our periodically forced discrete-time single patch epidemic model can generate multiple (coexisting) attractors. In this situation, the long-term disease dynamics depends on initial conditions.

Periodicity is not the only mechanism for generating multiple attractors. Migration and age-structure are known to induce multiple attractors in population models [5, 7, 9, 28, 29, 48, 50]. Also, epidemic models with "backward" bifurcations support multiple attractors [27, 47].

EXAMPLE 25. *Consider model* (7) *with 4-periodic constant recruitment function*

$$f(t, N) = k_t(1 - \gamma)$$

and

$$\phi\left(\frac{\alpha I}{N}\right) = e^{-\frac{\alpha I}{N}},$$

where

$$\alpha = 250, \quad \gamma = 0.4, \quad \sigma = 0.02, \quad k_0 = 1, \quad k_1 = 200, \quad k_2 = 1, \quad k_3 = 210.$$

Example 25 has two coexisting 4-cycle attractors, a "red" attractor at

$$\{(60.32, 52.44), (144.13, 3.57), (58.25, 56.14), (149.30, 1.29)\}$$

and a "black" attractor at

$$\{(60.32, 58.19), (144.13, 1.32), (58.25, 51.32), (149.30, 3.18)\}.$$

In this example, the total population is on a globally attracting 4-cycle, while the infective population is on multiple 4-cycle attractors. That is, the disease dynamics has multiple outcomes, while the total population has a single long-term dynamics. Figure 4 displays the two attracting 4-cycles.

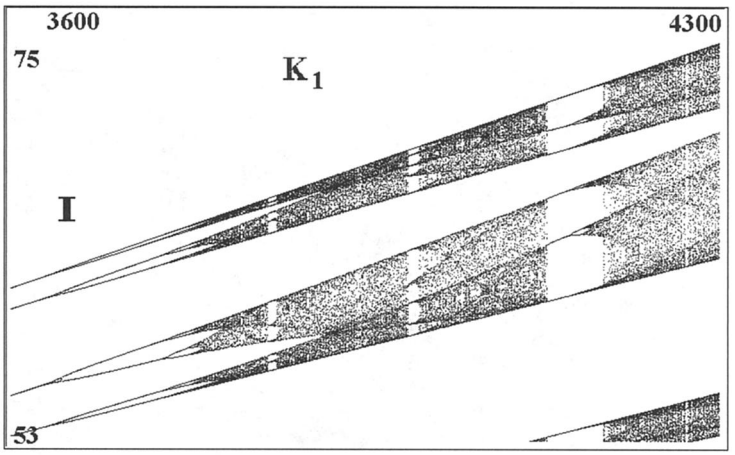

FIG. 5. *As k_1 varies between* 3600 *and* 4300, *the infective population in Example* 26 *undergoes period-doubling bifurcations route to chaos.*

9. Nonchaotic demographic dynamics generates chaotic disease dynamics. In constant environments, the demographic dynamics is capable of driving the disease dynamics [1, 2, 7, 8, 9]. That is, when the total population (in the absence of the disease) is on a cycle of period k, the population of infectives (in the presence of the disease) is also on a cycle of the same period k, albeit the amplitude of the total population is much larger than that of the infected population.

Our demographic equation with periodic constant or periodic Beverton–Holt or periodic geometric recruitment function can have either asymptotically bounded growth via globally attracting cycles (constant or Beverton–Holt models) or geometric growth (geometric model). In this section, we use numerical simulations to illustrate that the periodic epidemic model (4) can generate chaotic attractors where the periodic recruitment function is periodic constant or the periodic Beverton–Holt or periodic geometric function [39, 40, 41, 42, 43, 44, 45]. That is, in periodic environments, the demographic dynamics does not always drive the disease dynamics. We illustrate these cases in the following three examples.

EXAMPLE 26. *Consider model* (7) *with* 2*-periodic constant recruitment function*

$$f(t,N) = k_t(1-\gamma),$$

$$\phi\left(\frac{\alpha I}{N}\right) = e^{-\frac{\alpha I}{N}},$$

and

$$\alpha = 250, \quad \gamma = 0.44, \quad \sigma = 0.002, \quad k_0 = 1, \quad 3600 \le k_1 \le 4300.$$

Figure 5 shows parameter regimes of chaotic dynamics in the infective population of Example 26, where the total population is on a cyclic (nonchaotic) attractor. In this example, the recruitment function is a 2-periodic constant function. Next, we use numerical simulations to illustrate chaotic dynamics in the infective population where the recruitment function is the periodic Beverton–Holt model.

EXAMPLE 27. *Consider model* (7) *with* 2*-periodic geometric growth model*

$$f(t,N) = \frac{(1-\gamma)\mu k_t N(t)}{(1-\gamma)k_t + (\mu - 1 + \gamma)N(t)},$$

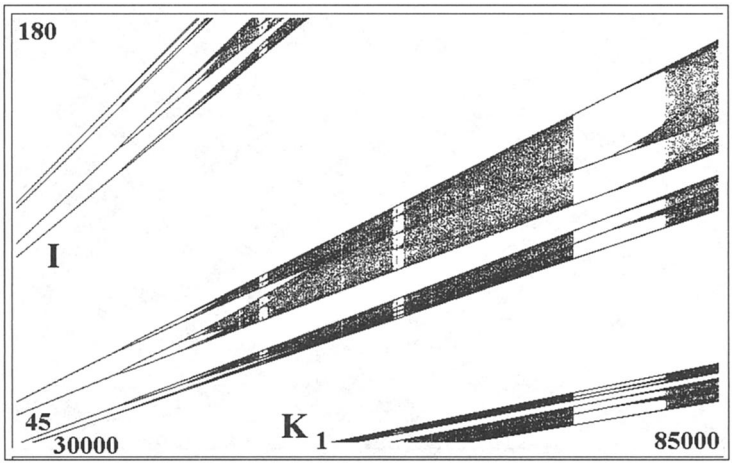

FIG. 6. *As k_1 varies between* 30000 *and* 85000, *the infective population in Example* 27 *undergoes period-doubling bifurcations route to chaos.*

$$\phi\left(\frac{\alpha I}{N}\right) = e^{-\frac{\alpha I}{N}},$$

and

$$\alpha = 250, \quad \gamma = 0.44, \quad \sigma = 0.002, \quad \mu = 2, \quad k_0 = 1, \quad 30000 \leq k_1 \leq 85000.$$

As we vary k_1 between 30000 and 85000, Figure 6 shows the infective population undergoing period-doubling bifurcations route to chaos. As in Figure 5, Figure 6 shows parameter regimes of chaotic dynamics in the infective population of Example 27, where the total population is governed by the 2-periodic Beverton–Holt model (nonchaotic dynamics). Next, we use numerical simulations to illustrate chaotic dynamics in the infective population where the recruitment function is the periodic geometric growth model.

EXAMPLE 28. *Consider model* (7) *with* 2*-periodic geometric growth model*

$$f(t, N) = \lambda_t N$$

and

$$\phi\left(\frac{\alpha I}{N}\right) = e^{-\frac{\alpha I}{N}},$$

where

$$\alpha = 250, \quad \gamma = 0.44, \quad \sigma = 0.002, \quad \lambda_0 = 0.0004, \quad 0.3 \leq \lambda_1 \leq 1.5.$$

As λ_1 varies between 0.3 and 1.5, the infective population in Example 28 undergoes period-doubling bifurcations route to chaos. As in Figures 5 and 6, Figure 7 shows parameter regimes of chaotic dynamics in the infective population of Example 28, where the total population is under geometric (nonchaotic) growth.

In periodic environments, Examples 26, 27, and 28 show that demographics dynamics does not always drive disease dynamics. In particular, they illustrate chaotic disease dynamics in the absence of chaotic dynamics in the demographic equation. These examples have only highlighted some of the complex interactions between disease and demographics dynamics in periodic environments.

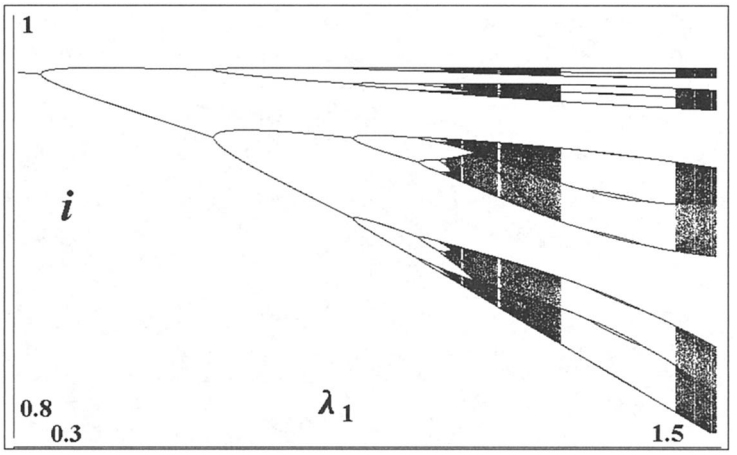

FIG. 7. *As* λ_1 *varies between* 0.3 *and* 1.5, *the infective population in Example* 28 *undergoes period-doubling bifurcations route to chaos.*

10. Conclusion. The study of the combined effects of seasonal trends and diseases on the extinction and persistence of discretely reproducing populations has received little attention. The focus has been on the impact of diseases on populations in constant (nonseasonal) environments [1, 2, 3, 7, 8, 9]. Most species live in seasonal environments, and the neglect of seasonal factors is apt to lead to a misunderstanding of how the population is interacting with its environment [26]. In this paper, we focus on the joint impact of periodic environments and disease epidemics on life-history outcomes of discretely reproducing populations. We formulated and analyzed a periodically forced discrete-time SIS epidemic model via the epidemic threshold parameter $\mathcal{R}_0$. We also investigated the relationship between the predisease invasion population dynamics and the diseases dynamics.

Fixed point (nonoscillatory) dynamics are rare in periodic environments. We use the periodic Beverton–Holt, the periodic constant, and the periodic Malthus (geometric growth) models as recruitment functions to highlight disease (uniform) persistence on globally attracting cycles whenever $\mathcal{R}_0 > 1$. The disease persists on fixed point attractors in the corresponding autonomous epidemic models [7, 8, 9].

In constant environments, Castillo-Chavez and Yakubu, in an earlier work, showed that the SIS discrete-time epidemic model supports only one attractor [7, 8, 9]. That is, the long-term epidemic dynamics is independent of initial population sizes. It is known that periodically forced (nonautonomous) population models without explicit disease dynamics are capable of generating multiple attractors via cusp bifurcations, where the corresponding autonomous models do not have multiple attractors [24]. In periodic environments, we use numerical simulations to show that the SIS model supports multiple attractors. That is, in periodic environments, the ultimate disease dynamics depends on initial population sizes. Seasonality is not the only mechanism for generating multiple attractors. Dispersal and age-structure are other factors that lead to the creation of multiple attractors in constant environments.

Castillo-Chavez and Yakubu, in [7, 8, 9], used the autonomous SIS discrete-time epidemic model to answer the following questions. Will the infective population survive? And if it does, will it settle on a particular attractor? What is the relationship between the population and epidemic attractors? Castillo-Chavez and Yakubu showed that in constant environments, infectives can survive on cyclic attractors. The period

of the (predisease invasion) population attractor is the same as the period of the infective population. In this paper, we show that it is possible for the disease dynamics to be chaotic, where the (predisease invasion) population is cyclic and nonchaotic. That is, with the advent of seasonality the demographic dynamics does not always drive the disease dynamics.

Acknowledgment. We thank the referees for useful comments and suggestions.

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