Mathematical Biology

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Structured population on two patches: modeling dispersal and delay

Abstract. We derive from the age-structured model a system of delay differential equations to describe the interaction of spatial dispersal (over two patches) and time delay (arising from the maturation period). Our model analysis shows that varying the immature death rate can alter the behavior of the homogeneous equilibria, leading to transient oscillations around an intermediate equilibrium and complicated dynamics (in the form of the coexistence of possibly stable synchronized periodic oscillations and unstable phase-locked oscillations) near the largest equilibrium.

1. Introduction

The purpose of this paper is two-fold:

I. To start the process of setting up a right model to describe the interaction of spatial dispersal/diffusion and time delays;
II. To analyze the resulting model and to illustrate the effect of the immature death rate on the global dynamics in structured populations in a patchy environment.

Given the death rate d and a birth function b, the dynamics of a single species population in a homogeneous environment is described by

$$\frac{du(t)}{dt} = -du(t) + b(u(t)) \tag{1.1}$$

or equivalently, in the form of logistic equations, by

$$\frac{du(t)}{dt} = u(t)[r - f(u(t))] \tag{1.2}$$

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for a certain constant r and a function f. Considering various facts causing delayed growth response, such as the hatching period, duration of gestation, maturation and slow replacement of food consumed, leads to the addition of a time delay $\tau > 0$ to (1.1) and (1.2), resulting in the following delay differential equation

$$\frac{du(t)}{dt} = -du(t) + b(u(t - \tau)) \tag{1.3}$$

or

$$\frac{du(t)}{dt} = u(t)[r - f(u(t - \tau))]. \tag{1.4}$$

Model equations (1.3) and (1.4) have been widely studied in the literature, and oscillations observed in laboratory experiments and in the real world have been successfully attributed to delayed rate response, see Cushing [1977], Kuang [1993], MacDonald [1979], May [1974, 1981] and Freedman and Gopalsamy [1986].

Spatial heterogeneity is ignored in model equations (1.1)–(1.4). Assuming the single species population is distributed over a two-patch environment, one naturally introduces two variables u_1 and u_2 to denote the population density in these two patches and describes the growth dynamics by

$$
\begin{aligned}
\frac{du_1(t)}{dt} &= -d_1 u_1(t) + b_1(u_1(t)) + D_2 u_2(t) - D_1 u_1(t), \\
\frac{du_2(t)}{dt} &= -d_2 u_2(t) + b_2(u_2(t)) + D_1 u_1(t) - D_2 u_2(t)
\end{aligned}
\tag{1.5}
$$

as a modification of (1.1), where d_i and b_i denote the death rates and birth functions in the appropriate patch, and D_i denotes the migration rate from one patch to another, see Levin [1974, 1976, 1986]. It has also been a common practice to modify equation (1.3) by adding the migration effect, as

$$
\begin{aligned}
\frac{du_1(t)}{dt} &= -d_1 u_1(t) + b_1(u_1(t - \tau)) + D_2 u_2(t) - D_1 u_1(t), \\
\frac{du_2(t)}{dt} &= -d_2 u_2(t) + b_2(u_2(t - \tau)) + D_1 u_1(t) - D_2 u_2(t)
\end{aligned}
\tag{1.6}
$$

or, in a continuous analog, by the following reaction-diffusion equation with delay

$$\frac{\partial u(t, x)}{\partial t} = \frac{\partial^2 u(t, x)}{\partial x^2} - du(t, x) + b(u(t - \tau, x)), \tag{1.7}$$

see Wu [1996] for some references. Unfortunately, there is a serious problem in the model equation (1.6) (or (1.7)). Namely, due to the spatial dispersal, the growth rate of the population at time t in the i-th patch (or at the spatial point x) should depend on the birth functions at time $t - \tau$ in both patches (or at other spatial points). Therefore, the term $b_i(u_i(t - \tau))$ (or $b(u(t - \tau, x))$) should be replaced by a more complicated function $B_i(u_1(t - \tau), u_2(t - \tau))$ of $u_1(t - \tau)$ and $u_2(t - \tau)$ (or by a functional $b(u(t - \tau, \cdot))$ of $u(t - \tau, \eta)$ for all η in the spatial domain). Deriving the concrete form of such a function is one of the main purposes of this paper.

Some progress has been made towards the above special "non-local" problem via a random walk argument by Britton [1990] and by Madras, Zou and Wu [1996]. See also Gourley and Britton [1993, 1996]. In this paper, we follow the idea of Smith [1994] to derive a system of delay differential equations

$$\frac{du_1(t)}{dt} = -d_1 u_1(t) + D_2 u_2(t) - D_1 u_1(t) + e^*(1-k)b_1(u_1(t-\tau))$$
$$+ e^* k b_2(u_2(t-\tau)),$$
$$\frac{du_2(t)}{dt} = -d_2 u_2(t) + D_1 u_1(t) - D_2 u_2(t) + e^* k b_1(u_1(t-\tau)) \qquad (1.8)$$
$$+ e^*(1-k)b_2(u_2(t-\tau))$$

for the mature population in both patches, from an age-structured population model (Metz and Diekmann [1986]) with spatial dispersal, where $(e^*)^{-1}$ is a function of the immature death rate, and the term $e^* k b_j(u_j(t-\tau))$ denotes the portion of the mature population which was born in the j-th patch at time $t-\tau$ but is in the i-th patch at the current time t. This term is usually ignored in the literature. See (2.9) for a more elaborate explanation.

Our preliminary analysis in Section 3 of the model equation (1.7) for a special case where the two patches are identical (leading to $d_1 = d_2$, $D_1 = D_2$, $b_1 = b_2$) shows that the immature death rate has a significant impact on the dynamics of the mature population. For the case where the birth function accounts for both the lack of "group defense" at low level of population and the crowding at high level of population, we show that (i) the model has 3 non-negative homogeneous equilibria $E_0 = (0, 0)$, $E_M = (x^*, x^*)$ and $E_L = (x^{**}, x^{**})$ with $0 < x^* < x^{**}$; (ii) varying the immature death rate can change the locations of E_M and E_L, lead to transient oscillations around E_M and to the coexistence of stable homogeneous periodic solutions and unstable phase-locked oscillations near E_L.

2. A two-patch model

The purpose of this section is to develop a model of a single species living in a two-patch environment. Let $u_i(t, a)$ denote the number of the species in patch i ($i = 1, 2$) at time t ($t \geq 0$) and at age a ($0 \leq a < \infty$). Then (see Diekmann and Metz [1986])

$$\begin{cases} \dfrac{\partial u_1(t,a)}{\partial t} + \dfrac{\partial u_1(t,a)}{\partial a} = -d_1(a)u_1(t,a) + D_2(a)u_2(t,a) - D_1(a)u_1(t,a), \\ \dfrac{\partial u_2(t,a)}{\partial t} + \dfrac{\partial u_2(t,a)}{\partial a} = -d_2(a)u_2(t,a) + D_1(a)u_1(t,a) - D_2(a)u_2(t,a). \end{cases}$$
$$(2.1)$$

Here $d_i(a)$ is the death rate of the individuals of age a in patch i and $D_j(a)u_j(t,a)$ corresponds to the dispersal of the species at age a from patch j to patch i, where $1 \leq i \neq j \leq 2$. We have assumed that there is no loss during migration from patch j to patch i, that is, all of those which leave patch j arrive at patch i safely.

Suppose that the population consists of two age-structured groups: immatures and matures, and denote the maturation age by $r \geq 0$. For $i = 1, 2$, we assume that

$$d_i(a) = \begin{cases} d_{i,I}(a) = d_I(a), & \text{for } 0 \leq a \leq r, \\ d_{i,m}(a) \equiv \text{constant}, & \text{for } a > r \end{cases} \tag{2.2}$$

and

$$D_i(a) = \begin{cases} D_{i,I}(a) = D_I(a), & \text{for } 0 \leq a \leq r, \\ D_{i,m} \equiv \text{constant}, & \text{for } a > r \end{cases} \tag{2.3}$$

where I stands for infants/immature and m stands for mature/adults. Note that we have assumed that the death rate of immatures is independent of the patch considered. This assumption is made just for the purpose of demonstrating the joint effect of maturation and spatial diffusion on the heterogeneity of the system in later sections. At a given time t, the number of adults in patch i is given by

$$w_i(t) = \int_r^\infty u_i(t, a)\, da, \tag{2.4}$$

and since only adults can give birth,

$$u_i(t, 0) = b_i(w_i(t)), \tag{2.5}$$

where $b_i(w)$ is the birth rate of the species in the i-th patch. By integrating (2.1) with respect to a from r to ∞, we have

$$\frac{d}{dt} w_i(t) = -\int_r^\infty \frac{\partial u_i}{\partial a}(t, a)\, da - \int_r^\infty d_i(a) u_i(t, a)\, da$$
$$+ \int_r^\infty D_j(a) u_j(t, a)\, da - \int_r^\infty D_i(a) u_i(t, a)\, da$$
$$= u_i(t, r) - d_{i,m} w_i(t) + D_{j,m} w_2(t) - D_{i,m} w_i(t),$$

where we have assumed $u_i(t, \infty) = 0$. Hence

$$\begin{cases} \dfrac{d}{dt} w_1(t) = -d_{1,m} w_1(t) + D_{2,m} w_2(t) - D_{1,m} w_1(t) + u_1(t, r), \\ \dfrac{d}{dt} w_2(t) = -d_{2,m} w_1(t) + D_{1,m} w_1(t) - D_{2,m} w_2(t) + u_2(t, r). \end{cases} \tag{2.6}$$

We now derive the formula for $u_i(t, r)$. Fix s and consider the function

$$V_i^s(t) = u_i(t, t - s), \quad \text{for } s \leq t \leq s + r \text{ and } i = 1, 2.$$

Then

$$\frac{d}{dt} V_i^s(t) = -d_i(t - s) V_i^s(t) + D_j(t - s) V_j^s(t) - D_i(t - s) V_i^s(t),$$
$$\text{for } t \geq s,\ 1 \leq i \neq j \leq 2.$$

Since $d_i(t - s) = d_I(t - s)$ for $i = 1, 2$ and $s \leq t \leq s + r$, we have

$$\frac{d}{dt} \left[V_1^s(t) + V_2^s(t) \right] = -d_I(t - s) \left[V_1^s(t) + V_2^s(t) \right].$$

Solving this linear equation and using (2.5), we get

$$V_1^s(t) + V_2^s(t) = e^{-\int_s^t d_I(\theta-s)\,d\theta} \left[V_1^s(s) + V_2^s(s)\right]$$
$$= e^{-\int_0^{t-s} d_I(a)\,da} \left[b_1(w_1(s)) + b_2(w_2(s))\right], \quad \text{for } s \le t \le s+r.$$

Hence

$$\frac{d}{dt} V_1^s(t) = -d_I(t-s)V_1^s(t) + D_2(t-s)\left[V_1^s(t) + V_2^s(t)\right]$$
$$-[D_1(t-s) + D_2(t-s)]V_1^s(t)$$
$$= -D^*(t-s)V_1^s(t) + D_2(t-s)e^{-\int_0^{t-s} d_I(a)\,da}\left[b_1(w_1(s)) + b_2(w_2(s))\right],$$

where $D^*(a) = d_I(a) + D_1(a) + D_2(a)$.

Solving the above for $V_1^s(t)$ yields

$$V_1^s(t) = e^{-\int_s^t D^*(\theta-s)\,d\theta} V_1^s(s)$$
$$+ \int_s^t e^{-\int_\xi^t D^*(\theta-s)\,d\theta} D_2(\xi-s)e^{-\int_0^{\xi-s} d_I(a)\,da}\,d\xi\ [b_1(w_1(s)) + b_2(w_2(s))]$$
$$= e^{-\int_0^{t-s} D^*(a)\,da} b_1(w_1(s))$$
$$+ \int_s^t e^{-\int_{\xi-s}^{t-s} D^*(a)\,da} D_2(\xi-s)e^{-\int_0^{\xi-s} d_I(a)\,da}\,d\xi\ [b_1(w_1(s)) + b_2(w_2(s))].$$

Let $\hat{D}(a) = D_1(a) + D_2(a)$. Then

$$u_1(t,r) = V_1^{t-r}(t)$$
$$= e^{-\int_0^r D^*(a)\,da} b_1(w_1(t-r))$$
$$+ \int_{t-r}^t e^{-\int_{\xi-t+r}^r D^*(a)\,da} D_2(\xi-t+r)\,e^{-\int_0^{\xi-t+r} d_I(a)\,da}\,d\xi$$
$$\times [b_1(w_1(t-r)) + b_2(w_2(t-r))]$$
$$= e^{-\int_0^r D^*(a)\,da} b_1(w_1(t-r))$$
$$+ e^{-\int_0^r d_I(a)\,da} \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_2(\theta)\,d\theta\ [b_1(w_1(t-r)) + b_2(w_2(t-r))].$$

Similarly,

$$u_2(t,r) = e^{-\int_0^r D^*(a)\,da} b_2(w_2(t-r))$$
$$+ e^{-\int_0^r d_I(a)\,da} \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta\ [b_1(w_1(t-r)) + b_2(w_2(t-r))].$$

Note that, using integration by parts, we have

$$\int_0^r e^{-\int_\theta^r [D_1(a)+D_2(a)]\,da} D_2(\theta)\,d\theta$$
$$= \int_0^r e^{-\int_\theta^r D_1(a)\,da} \left[e^{-\int_\theta^r D_2(a)\,da}\right]'\,d\theta$$

$$= \left[e^{-\int_\theta^r D_1(a)\,da} e^{-\int_\theta^r D_2(a)\,da} \right]_0^r - \int_0^r e^{-\int_\theta^r D_2(a)\,da} e^{-\int_\theta^r D_1(a)\,da} D_1(\theta)\,d\theta$$

$$= 1 - e^{-\int_0^r [D_1(a)+D_2(a)]\,da} - \int_0^r e^{-\int_\theta^r [D_1(a)+D_2(a)]\,da} D_1(\theta)\,d\theta.$$

Similarly,

$$\int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta = 1 - e^{-\int_0^r \hat{D}(a)\,da} - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_2(\theta)\,d\theta.$$

Substituting these into $u_1(t, r)$ and $u_2(t, r)$ leads to

$$
\begin{aligned}
u_1(t, r) &= e^{-\int_0^r D^*(a)\,da} b_1(w_1(t - r)) \\
&\quad + e^* \left[1 - e^{-\int_0^r \hat{D}(a)\,da} - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] \\
&\quad \times [b_1(w_1(t - r)) + b_2(w_2(t - r))] \\
&= \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] e^* b_1(w_1(t - r)) \\
&\quad + e^* \left[1 - e^{-\int_0^r \hat{D}(a)\,da} - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] b_2(w_2(t - r)) \\
&= \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] e^* b_1(w_1(t - r)) \\
&\quad + \left[\int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_2(\theta)\,d\theta \right] e^* b_2(w_2(t - r)),
\end{aligned}
\tag{2.7}
$$

where $e^* = e^{-\int_0^r d_I(a)\,da}$. Similarly,

$$
\begin{aligned}
u_2(t, r) &= \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_2(\theta)\,d\theta \right] e^* b_2(w_2(t - r)) \\
&\quad + \left[\int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] e^* b_1(w_1(t - r)).
\end{aligned}
\tag{2.8}
$$

Summarizing the above and using (2.6)–(2.8), we get the system of equations for $(w_1(t), w_2(t))$ as follows

$$
\left\{
\begin{aligned}
\frac{dw_1(t)}{dt} &= -d_{1,m} w_1(t) + D_{2,m} w_2(t) - D_{1,m} w_1(t) \\
&\quad + e^* \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] b_1(w_1(t - r)) \\
&\quad + e^* \left[\int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_2(\theta)\,d\theta \right] b_2(w_2(t - r)), \\
\frac{dw_2(t)}{dt} &= -d_{2,m} w_2(t) + D_{1,m} w_1(t) - D_{2,m} w_2(t) \\
&\quad + e^* \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_2(\theta)\,d\theta \right] b_2(w_2(t - r)) \\
&\quad + e^* \left[\int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_1(\theta)\,d\theta \right] b_1(w_1(t - r)).
\end{aligned}
\right.
\tag{2.9}
$$

Note that in the above system, the term $e^* \int_0^r e^{-\int_\theta^r \hat{D}(a)\,da} D_j(\theta)\,d\theta$ denotes the fraction of the mature population which was born at time $t - r$ in the j-th patch and is in the i-th patch at the current time t. This factor is usually ignored in the literature where a delay differential equation is used to model the dynamics of interacting species with time delay.

3. Two identical patches

In this section, we assume that the two patches are identical. Consequently, $d_{i,m} = d_m$, $D_{i,m} = D_m$, $b_i(w) = b(w)$ and $D_i(a) = D_I(a)$ for $i = 1, 2$ and for $0 \le a \le r$. Then

$$
\begin{cases}
\dfrac{dw_1(t)}{dt} = -d_m w_1(t) + D_m[w_2(t) - w_1(t)] \\
\qquad\qquad + e^*(1 - r^*)\, b(w_1(t - r)) + e^* r^*\, b(w_2(t - r)), \\
\dfrac{dw_2(t)}{dt} = -d_m w_2(t) + D_m[w_1(t) - w_2(t)] \\
\qquad\qquad + e^* r^*\, b(w_1(t - r)) + e^*(1 - r^*)\, b(w_2(t - r)),
\end{cases}
\tag{3.1}
$$

where

$$
\begin{aligned}
r^* &= \int_0^r e^{-2\int_\theta^r D_I(a)\,da} D_I(\theta)\,d\theta \\
&= \frac{1}{2} \int_0^r \frac{d}{d\theta}\left[e^{-2\int_\theta^r D_I(a)\,da} \right] d\theta \\
&= \frac{1}{2} \left[e^{-2\int_\theta^r D_I(a)\,da} \right]_0^r \\
&= \frac{1}{2} \left[1 - e^{-2\int_0^r D_I(a)\,da} \right].
\end{aligned}
\tag{3.2}
$$

Clearly $0 < r^* < \frac{1}{2}$. The equilibrium equations are:

$$
\begin{cases}
-d_m w_1 + D_m(w_2 - w_1) + e^*(1 - r^*)\, b(w_1) + e^* r^*\, b(w_2) = 0, \\
-d_m w_2 + D_m(w_1 - w_2) + e^* r^*\, b(w_1) + e^*(1 - r^*)\, b(w_2) = 0.
\end{cases}
\tag{3.3}
$$

In the remainder of this paper, we concentrate on the structure and the stability of homogeneous equilibria, and the associated Hopf bifurcation of homogeneous/heterogeneous periodic orbits. Here a homogeneous equilibrium (w_1, w_2) is one where $w_1 = w_2 = w$. The homogeneous equilibria are obtained from the solutions of the scalar equation

$$
d_m w = e^* b(w).
\tag{3.4}
$$

By the definition of e^*, we see that the maturation time r and the death rate $d_I(a)$, $a \in [0, r]$, for the immature population affect the structure of the homogeneous equilibria. In particular, the solution structure of (3.4) is determined by the ratio $d_m e^{\int_0^r d_I(a)\,da}$ over $\frac{b(w)}{w}$ for $w \ge 0$. In what follows, we let

$$
\alpha = e^{\int_0^r d_I(a)\,da} \left(= \frac{1}{e^*} \right).
\tag{3.5}
$$

Clearly, this parameter measures the death rate of the immature population during the maturation period.

A prototype of the birth function we are going to use is

$$b(w) = w^2 e^{-\beta w}, \quad \text{with } \beta > 0. \tag{3.6}$$

This describes the situation where the birth rate is small at both low and high levels of mature populations and large at the intermediate level of mature population. This occurs often due to lower mating rate and lack of "group defense" at low level of mature population and due to crowding at high level of mature population.

For the above birth function (see Figure 1), we can easily verify that

(i) if $\alpha > \frac{1}{\beta d_m e}$, then (3.4) has no positive solution;

(ii) if $\alpha = \frac{1}{\beta d_m e}$, then (3.4) has exactly one positive solution; and

(iii) if $\alpha < \frac{1}{\beta d_m e}$, then (3.4) has exactly two positive solutions.

In what follows, we will consider the case (iii) when (3.4) has three non-negative solutions: $0 < w^* < w^{**}$ with

$$0 \le b'(0)e^* < d_m < e^* b'(w^*) \quad \text{and} \quad b'(w^{**}) < 0. \tag{3.7}$$

Therefore, system (3.1) has three biologically meaningful homogeneous equilibria $E_0 = (0, 0)$, $E^* = (w^*, w^*)$ and $E^{**} = (w^{**}, w^{**})$.
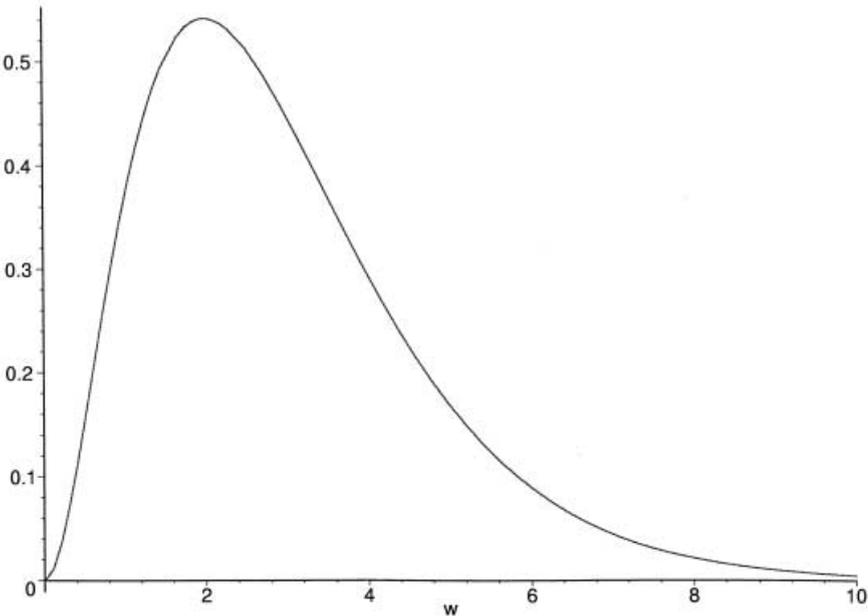

Fig. 1. The graph of $b(w) = w^2 e^{-\beta w}$ with $\beta = 1$.

The stability of a homogeneous equilibrium $(\tilde{w}, \tilde{w})$ is determined by the roots of the characteristic equation

$$
\begin{aligned}
0 &= \left| \begin{matrix} \lambda + d_m + D_m - e^*(1 - r^*)\, b'(\tilde{w})\, e^{-\lambda r} & -D_m - e^* r^*\, b'(\tilde{w})\, e^{-\lambda r} \\ -D_m - e^* r^*\, b'(\tilde{w})\, e^{-\lambda r} & \lambda + d_m + D_m - e^*(1 - r^*)\, b'(\tilde{w})\, e^{-\lambda r} \end{matrix} \right| \\
&= \left[\lambda + d_m + D_m - e^*(1 - r^*)\, b'(\tilde{w})\, e^{-\lambda r} \right]^2 - \left[D_m + e^* r^*\, b'(\tilde{w})\, e^{-\lambda r} \right]^2 \\
&= \left[\lambda + d_m - e^* b'(\tilde{w})\, e^{-\lambda r} \right] \left[\lambda + d_m + 2D_m - e^* e^{-2 \int_0^r D_I(a)\, da}\, b'(\tilde{w})\, e^{-\lambda r} \right]
\end{aligned}
$$

so that

$$
\lambda + d_m - e^* b'(\tilde{w})\, e^{-\lambda r} = 0 \tag{3.8}
$$

or

$$
\lambda + d_m + 2D_m - e^* e^{-2 \int_0^r D_I(a)\, da}\, b'(\tilde{w})\, e^{-\lambda r} = 0. \tag{3.9}
$$

The eigenvectors corresponding to the roots of (3.8) are homogeneous, whereas those corresponding to (3.9) are heterogeneous but symmetric with respect to the origin (i.e., $v_1 = -v_2$).

Notice that both (3.8) and (3.9) are of the form

$$
\lambda + u + v e^{-\lambda r} = 0 \tag{3.10}
$$

Necessary and sufficient conditions for all roots of (3.10) to have negative real parts are known, see for example, Hale and Verdyn Lunel [1993, Theorem A.5 on p. 416] and Kuang [1993].

3.1. Trivial equilibrium E_0: stability

The equilibrium $E_0 = (0, 0)$ is always asymptotically stable since $0 \le e^* b'(0) < d_m$ and $0 \le e^* b'(0)\, e^{-2 \int_0^r D_I(a)\, da} < d_m < d_m + 2D_m$.

3.2. Intermediate equilibrium E^*: transient oscillation

For the equilibrium $(w_1, w_2) = (w^*, w^*) = E^*$, since equation (3.8) with $\tilde{w} = w^*$ always has a positive real root, we conclude that this equilibrium is unstable.

In the limiting case when $r = 0$, equation (3.9) with $\tilde{w} = w^*$ has a negative root if

$$
D_m > \frac{1}{2}[b'(w^*) - d_m] \tag{3.11}
$$

and a positive root if

$$
0 < D_m < \frac{1}{2}[b'(w^*) - d_m]. \tag{3.12}
$$

Consequently, the equilibrium E^* is either a saddle (if condition (3.11) holds) or is an unstable node (if condition (3.12) holds). As the equilibrium $E^{**} = (w^{**}, w^{**})$ is clearly stable due to $b'(w^{**}) < 0$, we have the following phase portraits on the (w_1, w_2) plane (see Figures 2 and 3).

In particular, no oscillation near E^* will be observed when $r = 0$.

When $r > 0$, the situation is different. Assume that

$$e^*b'(w^*) \, e^{-2\int_0^r D_I(a)\,da} > d_m + 2D_m, \tag{3.13}$$

$$D_I(a) = D_m\frac{a}{r} \quad \text{for } 0 \le a \le r. \tag{3.14}$$

and

$$r > \frac{2\pi - \arccos\left(\frac{d_m}{e^*b'(w^*)}\right)}{\sqrt{[e^*b'(w^*)]^2 - d_m^2}}. \tag{3.15}$$

By using D_m as a bifurcation parameter, a standard analysis on equation (3.9) with $\tilde{w} = w^*$ shows that at $D_m = \tilde{D}_m = \tilde{D}_m(r)$, (3.9) has a pair of purely imaginary roots $\pm i\omega$ with

$$\omega = \sqrt{[e^*b'(w^*)e^{-\tilde{D}_m r}]^2 - (d_m + 2\tilde{D}_m)^2}. \tag{3.16}$$

Here $\tilde{D}_m(r)$ is the unique D_m such that

$$r\sqrt{[e^*b'(w^*)\, e^{-D_m r}]^2 - (d_m + 2D_m)^2} = 2\pi - \arccos\left(\frac{d_m + 2D_m}{e^*b'(w^*)\, e^{-D_m r}}\right) \tag{3.17}$$
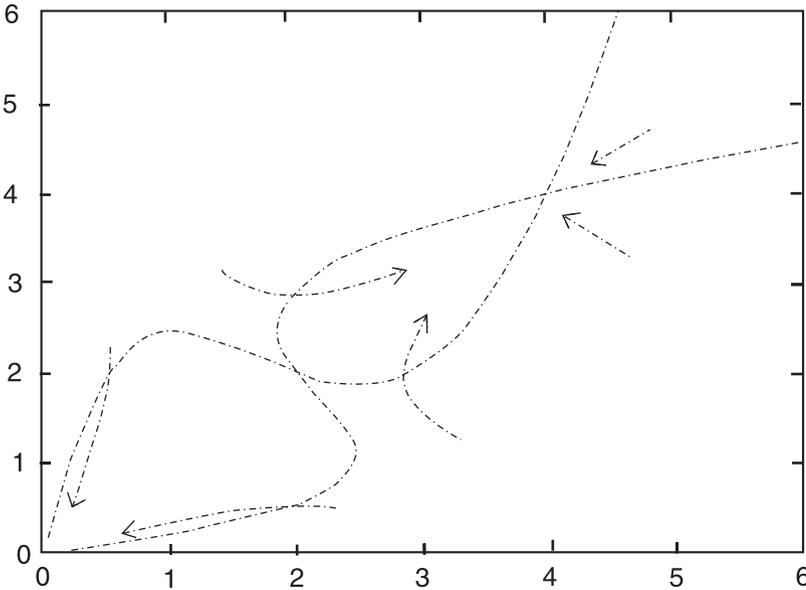

Fig. 2. Phase portrait of (3.1) with $r = 0$ and (3.10). Note that $r = 0$ implies $r^* = 0$, $e^* = 1$. Choose $w^* = 2$, $d_m = 1$ so that $\beta = \frac{1}{2}\ln 2$. RHS on (3.10) is $\frac{1}{2}[b'(w^*) - d_m] = \frac{1}{2}[1 - \ln 2] = 0.1534264097$. Choose $D_m = 0.2$. The isoclines intersect 3 times and there are 3 homogeneous equilibria.
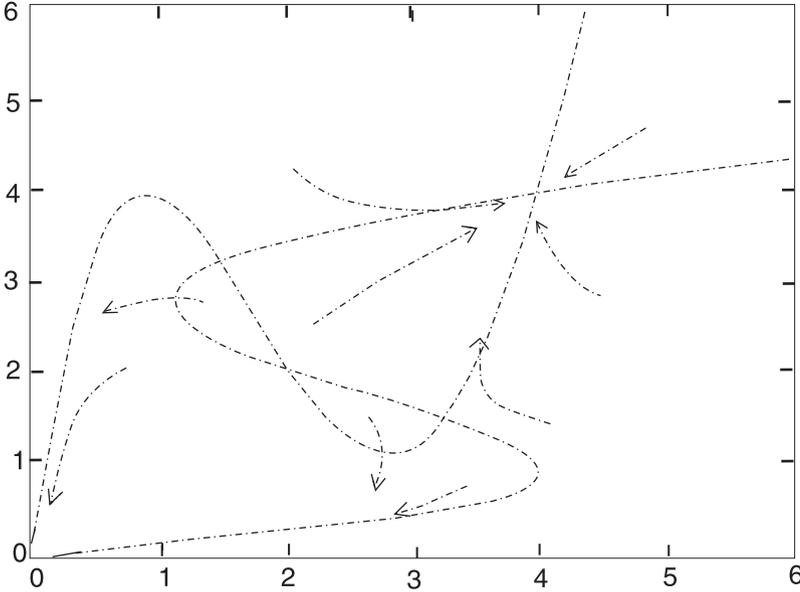
Fig. 3. Phase portrait of (3.1) with $r = 0$ and (3.11). Parameters are the same as in Figure 2, except $D_m = 0.1$. The isoclines intersect 5 times leading to 3 homogeneous equilibria and a pair of heterogeneous equilibria.

is satisfied. By thinking of the root λ as a function of D_m, one can easily check that the transversality condition for Hopf bifurcation is satisfied, namely

$$\text{Re}\lambda'(\tilde{D}_m) = -\frac{[2 + r(d_m + 2\tilde{D}_m)][1 + r(d_m + 2\tilde{D}_m)] + wr^2}{[1 + r(d_m + 2\tilde{D}_m)]^2 + \omega^2 r^2} < 0.$$

This implies that when D_m is close to $\tilde{D}_m$, there is a Hopf bifurcation of heterogeneous periodic solutions near the homogeneous equilibrium E^*. These bifurcated periodic solutions are unstable because equation (3.8) with $\tilde{w} = w^*$ has a positive real root. However, the existence of such periodic solutions causes transient oscillations for solutions near E^*, which cannot be observed when $r = 0$ (see Figure 4).

Summarizing the above discussions, we have

Theorem 3.1.

(i) *When $r = 0$, the intermediate equilibrium E^* is either a saddle or an unstable node and solutions of (3.1) near E^* do not oscillate around E^*.*

(ii) *Assume that (3.13) hold. Let the immature dispersal rate $D_I(a)$ be given by (3.14) and assume the maturation age r is sufficiently large so that (3.15) holds. For D_m close to $\tilde{D}_m$, the intermediate equilibrium E^* undergoes a Hopf bifurcation. The bifurcated heterogeneous periodic solutions lead to transient oscillations.*

3.3. Largest equilibrium E**: decreasing immature death leads to instability and oscillations

To discuss the stabilizing role of the immature death rate, we will use α defined in (3.5) as the bifurcation parameter in this section. We will see that there is a bifurcation at E^{**} as α decreases. Recall that $b'(w^{**}) < 0$.

Let $\theta = \theta(u) \in \left(\frac{\pi}{2}, \pi\right)$ be the unique number such that

$$-\frac{\theta}{ur} = \tan\theta.$$

It comes from assuming $\lambda = i\omega$, with $\omega > 0$, is a root of (3.10) and separate (3.10) into its real and imaginary parts. Define

$$\alpha_s = -\frac{b'(w^{**})}{\sqrt{d_m^2 + \left[\frac{\theta(d_m)}{r}\right]^2}} \qquad (3.18)$$

and

$$\alpha_p = -\frac{b'(w^{**})}{\sqrt{(d_m + 2D_m)^2 + \left[\frac{\theta(d_m+2D_m)}{r}\right]^2}} e^{-2\int_0^r D_I(a)\,da}. \qquad (3.19)$$

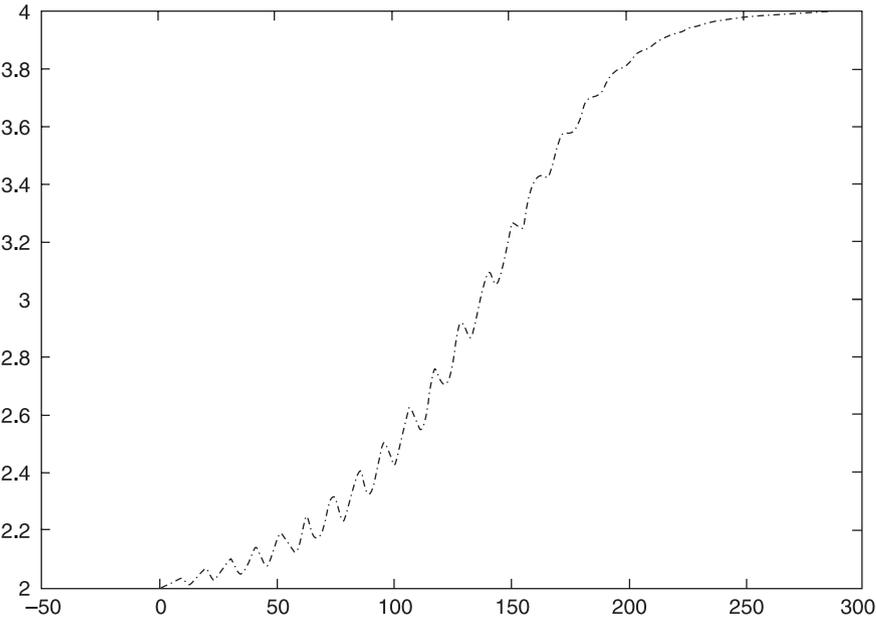**Fig. 4.** Transient oscillations for solutions near E^* when r is sufficiently large. This is a plot of $w_2(t)$ verses t. Initial condition is: $w_1(t)$ is linear with $w_1(-r) = 2$ and $w_1(0) = 2.2$ and $w_2(t) \equiv 2$ on $[-r, 0]$. Parameters are: $d_m = e^* = 0.9$, $r^* = 0.1$, $\beta = \frac{1}{2}\ln 2$, $r = 10$ and $D_m = 0.071$. Note that, $w^* = 2$ and $w^{**} = 4$.
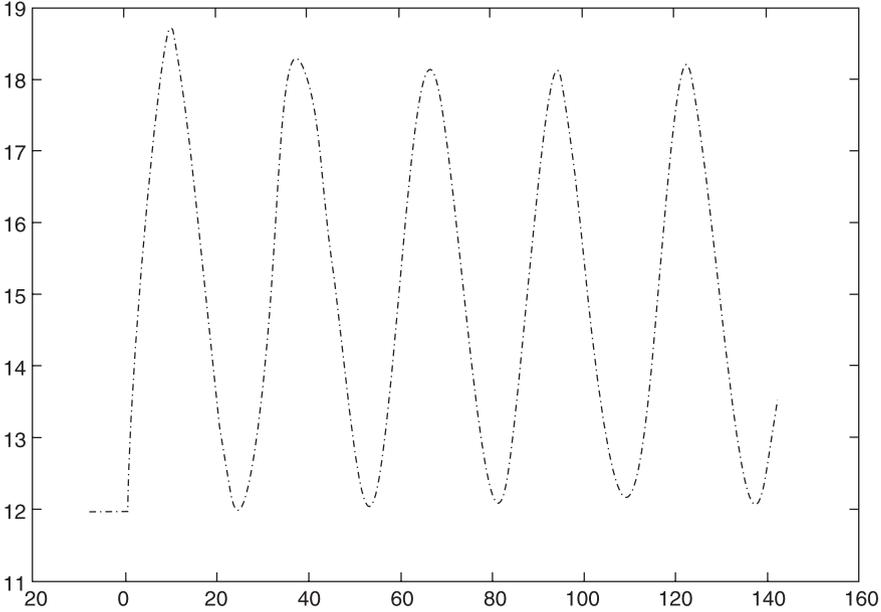
Fig. 5. Hopf bifurcation of stable synchronized periodic solutions from E^{**}. This is a plot of $w_1(t)$ verses t. Initial condition is: $(w_1(t), w_2(t)) = (12.0, 13.0)$ for $t \in [-r, 0]$. Parameters are: $d_m = 0.08$, $D_m = 0.01$, $r = 8.5$, $r^* = 0.1$, $e^* = 0.9$, $\beta = \frac{1}{2}\ln 2$.

Note that α_s (resp. α_p) is the first value of the parameter α for which (3.8) (resp. (3.9)) has a pair of purely imaginary roots. The monotonicity of θ implies that $0 < \alpha_p < \alpha_s$.

Applying the result in Hale and Verduyn Lunel [1993, Theorem A.5 on p. 416], it is easy to show that if $\alpha > \alpha_s$, then all zeros of (3.8) and (3.9) have negative real parts. Thus $E^{**} = (w^{**}, w^{**})$ is asymptotically stable when $\alpha > \alpha_s$. However, at $\alpha = \alpha_s$, (3.8) has a pair of purely imaginary zeros and the standard Hopf bifurcation theorem (see, Hassard, Kazarinoff and Yan [1981]) shows the existence of a Hopf bifurcation of periodic solutions near E^{**}. Such periodic solutions must be homogeneous (synchronized) as the homogeneous solutions (w_1, w_2) with $w = w_1 = w_2$ are described by the scalar equation

$$\frac{dw(t)}{dt} = -d_m w(t) + \frac{1}{\alpha}b(w(t - r))$$

which has a Hopf bifurcation at $\alpha = \alpha_s$. Numerical simulations reported in Figure 5 shows that these homogeneous periodic solutions bifurcated from E^{**} can be stable.

On the other hand, one can also apply Theorem 2.1 in Wu [1998] to show that at $\alpha = \alpha_p$, system (3.1) has another branch of periodic solutions $w(t) = (w_1(t), w_2(t))$ bifurcating from E^{**}, and such periodic solutions must be phase-locked in the sense that $w_1(t) = w_2(t - \frac{T}{2})$ for the minimal period T of $w(t)$.

These phase-locked periodic solutions must be unstable since (3.8) with $\tilde{w} = w^{**}$ has a root with positive real part.

In summary, we have

Theorem 3.2. *Let α_s and α_p be defined as in (3.18) and (3.19). Then $\alpha_s > \alpha_p$.*

   (i) *The largest equilibrium E^{**} is asymptotically stable for $\alpha > \alpha_s$.*
  (ii) *At $\alpha = \alpha_s$, system (3.1) has a Hopf bifurcation of (possibly stable) homogeneous periodic solutions from E^{**}.*
 (iii) *At $\alpha = \alpha_p$, (3.1) has a Hopf bifurcation of unstable phase-locked periodic solutions from E^{**}.*

4. Discussion

In this paper we developed a model for an age-structured population in a patchy (two patches) environment. The model equation (2.9) contains a term representing the fraction of the mature population which was born at time $t - r$ in one patch and has moved to the other patch at time t. This term is usually ignored in the literature. Similar ideas can be used to develop a model for an age-structured population in a continuous environment (cf. So, Wu and Zou [2000]). This leads to a reaction-diffusion equation with time delays and non-local effects. It is our hope that these equations will be useful in modeling real populations in future work.

The analysis carried out in Section 3 shows that periodic solutions are possible through Hopf bifurcation. Those periodic solutions that bifurcate from E^*, the intermediate equilibrium, will be unstable and heterogeneous. There are two Hopf bifurcations at E^{**}, the largest equilibrium. The first one leads to (possibly) stable homogeneous periodic solutions whereas the second one leads to unstable phase-locked periodic solutions. The global dynamics is far from completely understood at this moment.

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