The Effect of Diffusion on the Time Varying Logistic Population Growth

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Abstract—In this paper, we consider the effect of diffusion on the species that live in changing patches environment. Different from the former studies [1–4], we pay attention to the more important situation in conservation biology that species live in a weak patches environment, in the sense that species in some of the isolated patches will be extinct without the contribution from other patches. We obtain an interesting result: the identical species can persist for some diffusion rates, and can also vanish for another set of restriction on diffusion rates. © 1998 Elsevier Science Ltd. All rights reserved.

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1. INTRODUCTION

One of the most important challenges facing ecologists over the next decades is to help with the conservation of endangered species and ecosystems. As has been recognized increasingly within ecology, in general, and in conservation, in particular, meeting these challenges will require including the role of spatial structure in the models that are used.

Recently, some authors studied the influence of diffusion on the time dependent single species dynamics (see [1–3]). Mahbuba and Chen [1] considered the following system:

$$\dot{x}_i = x_i \left\{ b_i(t) - a_i(t) x_i \right\} + D_i(t)(x_j - x_i), \qquad i, j = 1, 2. \tag{*}$$

If $b_i(t)$ and $a_i(t)$ $(i = 1, 2)$ are all positive periodic functions, then system (*) possesses a globally stable positive periodic solution for any positive diffusive rates $D_1(t)$ and $D_2(t)$.

In [2], Wang and others studied the global stability of system (*) under the assumption that the functions $a_i(t)$ and $b_i(t)$ $(i = 1, 2)$ are continuous and bounded above and below by positive constants, $D_i(t)$ $(i = 1, 2)$ continuous, nonnegative, and bounded by positive constants.

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In [1,2], the authors always suppose that the species has positive intrinsic growth rates $b_i(t)$ ($i = 1, 2$) in each patch. But the most endangered species live in a weak patches environment, in the sense that in some of the isolated patches, the species will vanish without the contribution from other patches. This fact urged us to consider the effect of diffusion on the permanence and extinction of single species living in a weak environments. As we shall see later, the species can persist for some diffusion rates and can also vanish for another set of diffusion rates. These results can be used for explaining the biologically interesting problem: to what extent does diffusion lead to the permanence or extinction of species which could not persist within some isolated patches.

On the studies of the giant panda protection projects [5–7], we often face the fact that giant pandas sometimes migrate from one patch to another for finding food, mating, etc. In order to protect the rare species, we should investigate the circumstance of every patch and control the diffusive rates among different patches.

The organization of this paper is as follows. In the next section, a model is given, its permanence and extinction are both considered. We obtain that the system can be made either permanent or extinct under different appropriate diffusion conditions, even if the corresponding isolated patches are not persistent.

In Section 3, it is shown to have a unique globally asymptotically stable positive periodic solution provided that the system is permanent. The biological meaning of the results obtained in Sections 2 and 3 are discussed in Section 4.

2. MODEL, PERMANENCE, AND DISTINCTION

We consider the system as composed of patches connected by discrete diffusions, each patch is assumed to be occupied by a single species as follows:

$$\dot{x}_i = x_i \{b_i(t) - a_i(t)x_i\} + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i), \qquad (i,j = 1, 2, \ldots, n), \qquad (1)$$

where x_i ($i = 1, 2, \ldots, n$), defined in $R_+^n = \{(x_1, x_2, \ldots, x_n) \in R^n \mid x_1 \geq 0, x_2 \geq 0, \ldots, x_n \geq 0\}$ is the number of species x in patch i. Functions $b_i(t)$, $a_i(t)$, and $D_{ij}(t)$ ($i = 1, 2, \ldots, n$) are all continuous functions of time $t \in (-\infty, +\infty)$ and are assumed to be periodic with common period $\omega > 0$. $b_i(t)$ is the intrinsic growth rate for species x in patch i; $a_i(t)$ (positive) represents the self-inhibition coefficient; and $D_{ij}(t)$ (positive) is the diffusion coefficient of species x from patch j to patch i.

Throughout this paper, we assume that $a_i(t) > 0$, $D_{ij}(t) > 0$ ($i \neq j$), and $D_{ii}(t) = 0$ ($i, j = 1, 2, \ldots, n$)

We call system (1) persistent if all solutions of (1) with positive initial values satisfy $\lim_{t \to \infty} \inf x_i(t) > 0$ ($i = 1, 2, \ldots, n$). System (1) is said to be permanent if there exists a compact set K in the interior of R_+^n, such that all solutions starting in the interior of R_+^n ultimately enter K.

To simplify writing, we introduce the following notations: if $g(t)$ is a continuous ω-periodic function defined on $(-\infty, +\infty)$, we set

$$[g] = \omega^{-1} \int_0^\omega g(t)\, dt, \qquad g^M = \max_t g(t), \qquad g^L = \min_t g(t).$$

To prove the permanence of system (1), we need information on the well-known time dependent logistic model

$$\dot{N} = N\{b(t) - a(t)N\}, \qquad (2)$$

where $b(t)$ and $a(t)$ (positive) are continuous periodic functions with common period $\omega > 0$.

Lemma.

(i) *Suppose that $[b] > 0$, then (2) has a unique positive, globally asymptotically stable ω-periodic solution.*

(ii) *Suppose that* $[b] < 0$, *then all solutions* $N(t)$ *of (2) with positive initial values satisfy* $\lim_{t\to\infty} N(t) = 0$.

This result can be seen by direct integration (or see [8]).

THEOREM 1. *Given any* $\xi_i > 0$ $(i = 1, 2, \ldots, n)$, *the initial value problem*

$$\dot{x}_i = x_i\{b_i(t) - a_i(t)x_i\} + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i),$$

$$x_i(0) = \xi_i, \qquad i, j = 1, 2, \ldots, n, \tag{3}$$

has a unique solution $x(t) = (x_1(t), x_2(t), \ldots, x_n(t))$ *which exists for all* $t \geq 0$. *Moreover, there exists* $M > 0$, $\tau > 0$, *such that*

$$0 < x_i(t) \leq M, \qquad for \ t \geq \tau, \tag{4}$$

the region $D = \{(x_1, x_2, \ldots, x_n) \mid 0 < x_i \leq M, \ i = 1, 2, \ldots, n\}$ *is positively invariant with respect (1).*

PROOF. Define

$$V(x(t)) = \max_{1 \leq i \leq n} \{x_i(t)\}. \tag{5}$$

Calculating the upper-right derivative of $V(x(t))$ along the positive solution of (3), we have

$$D^+V \leq V \max_{1 \leq i \leq n} \{b_i(t) - a_i(t)V\}.$$

Denote $M = \max_{1 \leq i \leq n}\{(|b_i^M| + 1)/a_i^L\}$. If $V \geq M$, then $D^+V \leq -V$. Hence, there exists $\tau = \tau(x_1(0), x_2(0), \ldots, x_n(0)) > 0$, such that $V(t) \leq M$, for all $t \geq \tau$, which means that $x_i(t) \leq M$ $(i = 1, 2, \ldots, n)$, for all $t \geq \tau$ if $x(t)$ exists. But, the ultimately boundness implies that $x(t)$ exists for all $t > 0$. Furthermore,

$$\dot{x}_i\big|_{x_i=M, x_i \geq x_j} < M \left(b_i^M - a_i^L M\right) < 0.$$

Hence, all solutions of (3) initiating in boundary of D enter the region D for $t \geq 0$, so D is positively invariant with respect (1). This completes the proof.

REMARK 1. Suppose that $b_i(t) < 0$ $(i = 1, 2, \ldots, n)$, then $b_i^M < 0$ and

$$\dot{x}_i\big|_{x_i=\delta, x_i \geq x_j} < \delta \left(b_i^M - a_i^L \delta\right) < 0,$$

for any positive number δ. From the proof of above theorem, we have $x_i(t) \to 0$ as $t \to \infty$. Therefore, system (1) will be extinct for any diffusion rate $D_{ij}(t) \geq 0$ $(i, j = 1, 2, \ldots, n)$.

A consequence of Theorem 1 is that for $\xi_i > 0$ $(i = 1, 2, \ldots, n)$, the solution of (3) is ultimately bounded above. We will show that this solution is also ultimately bounded below, away from zero, provided that the one of the following conditions is satisfied.

(H1) There exists i_0 $(1 \leq i_0 \leq n)$, such that $[b_{i_0}(t)] > [\sum_{j=1}^{n} D_{i_0 j}(t)]$.

(H2) $[\phi(t)] > 0$, where $\phi(t) = \min_{1 \leq i \leq n}\{b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t)\}$.

THEOREM 2. *Suppose that (H1) or (H2) holds, then there exists* δ_i, $0 < \delta_i < M$, *and* $\tau \geq 0$, *such that the solution of (3) satisfies*

$$x_i(t) \geq \delta_i, \tag{6}$$

for $i = 1, 2, \ldots, n$ *and* $t \geq \tau$, *where* δ_i $(i = 1, 2, \ldots, n)$ *depend on the various Assumptions (H1) and (H2).*

PROOF I. Suppose that (H1) holds, we have

$$\dot{x}_{i_0} > x_{i_0} \left\{ \left(b_{i_0}(t) - \sum_{j=1}^{n} D_{i_0 j}(t) \right) - a_{i_0}(t)x_{i_0} \right\},$$

by the lemma, the logistic equation

$$\dot{u} = u\left\{\left(b_{i_0}(t) - \sum_{j=1}^{n} D_{i_0 j}(t)\right) - a_{i_0}(t)u\right\} \tag{7}$$

has a unique positive globally asymptotically stable ω-periodic solution $\tilde{u}(t) \subset [\tilde{\delta}_{i_0}, \tilde{k}_{i_0}]$ $(0 < \tilde{\delta}_{i_0} < \tilde{k}_{i_0})$. Let $u(t)$ be the solution of (7) with $u(0) = x_{i_0}(0)$, by comparison theorem of differential equation, $x_{i_0}(t) \geq u(t) > 0$. Take $\epsilon_{i_0} = (\tilde{\delta}_{i_0})/2$, then there exists $T_{i_0} = T_{i_0}(x_1(0), x_2(0), \ldots, x_n(0))$, such that

$$|u(t) - \tilde{u}(t)| < \epsilon_{i_0}, \qquad \text{for } t \geq T_{i_0}.$$

Then

$$x_{i_0}(t) \geq u(t) > \tilde{u}(t) - \epsilon_{i_0} \geq \frac{\tilde{\delta}_{i_0}}{2} = \delta_{i_0}.$$

Moreover, for every $j \neq i_0$, we have

$$\dot{x}_j \geq -a_j^M x_j^2 + \left(b_j^L - \sum_{k=1}^{n} D_{jk}^M\right) x_j + D_{ji_0}^L \delta_{i_0} = f(x_j), \qquad \text{for } t \geq T_{i_0}.$$

The algebraic equation

$$a_j^M x_j^2 - \left(b_j^L - \sum_{k=1}^{n} D_{jk}^M\right) x_j - D_{ji_0}^L \delta_{i_0} = 0$$

gives us one positive root

$$\tilde{x}_j = \frac{b_j^L - \sum\limits_{k=1}^{n} D_{jk}^M + \sqrt{\left(b_j^L - \sum\limits_{k=1}^{n} D_{jk}^M\right)^2 + 4a_j^M D_{ji_0}^L \delta_{i_0}}}{2a_j^M}.$$

Clearly, $f(x_j) > 0$ for every positive number x_j $(0 \leq x_j < \tilde{x}_j)$. Choose δ_j $(0 < \delta_j < \tilde{x}_j)$, $\dot{x}_j|_{x_j=\delta_j} > f(\delta_j) > 0$, if $x_j(T_{i_0}) \geq \delta_j$, then it also holds for $t \geq T_{i_0}$; if $x_j(T_{i_0}) < \delta_j$, then

$$\dot{x}_j(T_{i_0}) \geq \inf\{f(x_j) \mid 0 \leq x_j < \delta_j\} > 0,$$

there must exist T_j $(\geq T_{i_0})$, such that $x_j(t) \geq \delta_j$ for $t \geq T_j$. Therefore, (6) applies with $\tau = \max_{1 \leq j \leq n} T_j$.

PROOF II. Choose function

$$\rho = \rho(x_1, x_2, \ldots, x_n) = x_1 + x_2 + \cdots + x_n,$$

calculating the derivative of ρ along the solution of (1), we have

$$\dot{\rho}|_{(1)} = \sum_{i=1}^{n}\left\{b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t)\right\} x_i - \sum_{i=1}^{n} a_i(t)x_i^2 \geq \rho\left(\phi(t) - a(t)\rho\right),$$

where $a(t) = \max_{1 \leq i \leq n}\{a_i(t)\}$. By the lemma and (H2), the logistic equation

$$\dot{v} = v\{\phi(t) - a(t)v\} \tag{8}$$

has a unique positive globally asymptotically stable ω-periodic solution $\tilde{v}(t) \subset [p, q]$ $(0 < p < q)$. Let $v(t)$ be the solution of (8) with $v(0) = \sum_{i=1}^{n} x_i(0)$, by comparison theorem of differential

equation, $\rho(t) \geq v(t) > 0$. Take $\epsilon = p/2$, then there exists $T = T(x_1(0), x_2(0), \ldots, x_n(0))$, such that

$$|v(t) - \tilde{v}(t)| < \epsilon, \qquad \text{for } t \geq T.$$

Then

$$x_1(t) + x_2(t) + \cdots + x_n(t) > \tilde{v} - \epsilon \geq \frac{p}{2} = \eta, \qquad \text{for } t \geq T. \tag{9}$$

Hence,

$$\dot{x}_i = x_i \left\{ b_i(t) - \sum_{j=1}^{n} D_{ij}(t) - a_i(t)x_i \right\} + \sum_{j=1}^{n} D_{ij}(t)x_j$$

$$> x_i \left(b_i^L - D_0 - \sum_{j=1}^{n} D_{ij}^M - a_i^M x_i \right) + D_0 \eta$$

or

$$\dot{x}_i > -a_i^M x_i^2 - \left(\sum_{j=1}^{n} D_{ij}^M + D_0 - b_i^L \right) x_i + D_0 \eta,$$

for $t \geq T$ and $i = 1, 2, \ldots, n$, where $D_0 = \min_{\substack{1 \leq i,j \leq n \\ i \neq j}} \{D_{ij}^L\} > 0$.

The algebraic equation

$$a_i^M x_i^2 + \left(\sum_{j=1}^{n} D_{ij}^M + D_0 - b_i^L \right) x_i - D_0 \eta = 0$$

gives us one positive root

$$\tilde{x}_i = \frac{b_i^L - D_0 - \sum\limits_{j=1}^{n} D_{ij}^M + \sqrt{\left(b_i^L - D_0 - \sum\limits_{j=1}^{n} D_{ij}^M \right)^2 + 4D_0 \eta a_i^M}}{2a_i^M}, \qquad (i = 1, 2, \ldots, n).$$

An entirely similar argument, as Proof I shows, is that there exists δ_i ($\delta_i < M, i = 1, 2, \ldots, n$) and T' ($\geq T$) such that (6) holds for $\tau = T'$. This completes the proof.

Applying the above theorem to two patches system, we obtain the following result.

COROLLARY 1. *If $n = 2$ and one of the following Conditions (A1)–(A4) holds:*

(A1) $[b_1] > [D_{12}]$;

(A2) $[b_2] > [D_{21}]$;

(A3) $b_1(t) + D_{21}(t) - D_{12}(t) \geq b_2(t) + D_{12}(t) - D_{21}(t)$ and $[b_2(t) + D_{12}(t) - D_{21}(t)] > 0$;

(A4) $b_2(t) + D_{12}(t) - D_{21}(t) \geq b_1(t) + D_{21}(t) - D_{12}(t)$ and $[b_1(t) + D_{21}(t) - D_{12}(t)] > 0$.

Then the result of Theorem 2 holds for $i = 1, 2$.

Theorems 1 and 2 have established that, under one of Assumptions (H1) or (H2), there exist positive constants m and M, the solution of (1) with positive initial values ultimately enter the rectangular region $\Omega = \{(x_1, x_2, \ldots, x_n) \mid m \leq x_i \leq M, \ i = 1, 2, \ldots, n\}$, therefore, the population is permanent.

REMARK 2. According to the proof of Theorem 2, if species x is permanent in a fixed patch i, then species x is also permanent in other patches for any diffusion rates $D_{ji}(t)$ ($i, j = 1, 2, \ldots, n$). Assumption (H1) implies that if the average of the sum of diffusion rates from patch j ($j = 1, 2, \ldots, n$) to patch i is less than the intrinsic growth rate of patch i ($i \neq j$), then species x is permanent even if the isolated patch j is not persistent.

REMARK 3. Let us consider the simplest case where the patches are identical, that is $b_i(t) = b(t)$, $a_i(t) = a(t)$, and $D_{ij}(t) = D_{ji}(t)$ $(i, j = 1, 2, \ldots, n)$. In this case, the restriction on $D_{ij}(t)$ has been dropped, Assumption (H2) becomes simply

$$[b] > 0. \tag{10}$$

This condition ensures that each isolated patch is permanent (by the lemma, each isolated patch has a unique globally asymptotically stable positive ω-periodic solution). Therefore, the above result implies that the system with the identical patch continues to be permanent.

REMARK 4. Here we discuss a simple example that illustrates the biological consequence of the result on Theorem 2:

$$
\begin{aligned}
\dot{x}_1 &= x_1 \left[1 + \frac{1}{4} \sin t - a_1(t) x_1 \right] + D_{12}(t)(x_2 - x_1), \\
\dot{x}_2 &= x_2 \left[-\frac{1}{4} + \frac{1}{4} \sin t - a_2(t) x_2 \right] + D_{21}(t)(x_1 - x_2),
\end{aligned}
\tag{11}
$$

where $a_i(t)$ and $D_{ij}(t)$ $(i, j = 1, 2;\ i \neq j)$ are all positive continuous periodic functions with common period 2π.

If the patches are isolated from each other, it is clear that species x will be permanent in patch 1 and will not be persistent in patch 2. Conditions (A1) or (A3) holds for (11) provided $[D_{12}] < 1$ or $1/4 < [D_{12}(t) - D_{21}(t)]$, $D_{12}(t) - D_{21}(t) \leq 5/8$, respectively. Corollary 1 says that system (11) is permanent. This means that by appropriately choosing diffusion coefficient $[D_{12}] < 1$ or $1/4 < [D_{12}(t) - D_{21}(t)]$, $D_{12}(t) - D_{21}(t) \leq 5/8$, if the stabilizing effect in patch 1 is stronger than the destabilizing effect in patch 2, then the dispersal acts as a stabilizing influence and causes the overall system (11) to be permanent.

Next, we will consider the extinction of system (1). Denote

$$\psi(t) = \max_{1 \leq i \leq n} \left\{ b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t) \right\}.$$

THEOREM 3. *Suppose that $[\psi(t)] < 0$ holds, then the solution of (3) satisfies*

$$x_i(t) \to 0, \qquad \text{as } t \to \infty. \tag{12}$$

PROOF. Consider the function $\rho = \sum_{i=1}^{n} x_i$ defined in Theorem 2, calculating the derivative of function ρ along the solution of (1)

$$\dot{\rho}|_{(1)} = \sum_{i=1}^{n} \left\{ b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t) \right\} x_i - \sum_{i=1}^{n} a_i(t) x_i^2 < \psi(t)\rho.$$

Let $u(t)$ be the solution of the equation

$$\dot{u} = \psi(t) u,$$

with $u(0) = \rho(0)$. By comparison theorem of differential equation, $\rho(t) \leq \rho(0) \exp(\int_0^t \psi(t)\, dt)$. Since $[\psi(t)] < 0$, $\int_0^t \psi(t)\, dt \to -\infty$, as $t \to \infty$. Consequently, $\rho = \sum_{i=1}^{n} x_i \to 0$, as $t \to \infty$. So $x_i(t) \to 0$, as $t \to \infty$. This completes the proof.

COROLLARY 2. *If $n = 2$ and the following Conditions (A5) or (A6) holds,*

(A5) $b_1(t) + D_{21}(t) - D_{12}(t) \geq b_2(t) + D_{12}(t) - D_{21}(t)$ *and* $[b_1(t) + D_{21}(t) - D_{12}(t)] < 0;$

(A6) $b_1(t) + D_{21}(t) - D_{12}(t) \leq b_2(t) + D_{12}(t) - D_{21}(t)$ *and* $b_2(t) + D_{12}(t) - D_{21}(t) < 0.$

Then $x_i(t) \to 0$ $(i = 1, 2)$, as $t \to \infty$.

In fact, Conditions (A5) or (A6) implies $\psi(t) = b_1(t) + D_{21}(t) - D_{12}(t)$ or $\psi(t) = b_2(t) + D_{12}(t) - D_{21}(t)$, respectively. By applying Theorem 3, the corollary is true.

REMARK 5. In the completely identical case of Remark 3, the assumptions of Theorem 3 become simply

$$[b] < 0. \tag{13}$$

By the lemma, this condition ensures that each isolated patch is extinct. Therefore, the identical patch continues to be extinct.

REMARK 6. Consider a simple example, note that the intrinsic growth rate for species x in patch 2 is less than that in Remark 4:

$$
\begin{aligned}
\dot{x}_1 &= x_1 \left[1 + \frac{1}{4} \sin t - a_1(t)x_1 \right] + D_{12}(t)(x_2 - x_1), \\
\dot{x}_2 &= x_2 \left[-2 + \frac{1}{4} \sin t - a_2(t)x_2 \right] + D_{21}(t)(x_1 - x_2),
\end{aligned}
\tag{14}
$$

where $a_i(t)$ and $D_{ij}(t)$ $(i, j = 1, 2, i \neq j)$ are all continuous positive periodic functions with common period 2π.

System (14) without diffusion (two isolated patches) will be permanent in patch 1 and will not be persistent in patch 2 as Remark 4. Condition (A5) holds, if $1 < [D_{12}(t) - D_{21}(t)]$ and $D_{12}(t) - D_{21}(t) \leq 3/2$. Theorem 3 implies that system (14) goes extinct. This means that if the inherent net birth rate of species x in patch 2 is negative and small enough, then the stabilizing effect in system (14) is weaker than the destabilizing influence and causes the overall system (14) to go extinct. On the other hand, if $[D_{12}] < 1$, then (A1) holds. By Theorem 2, system (1) is permanent for any diffusion rate $D_{21}(t) > 0$.

The above conclusion implies that the diffusion rates play an important role on the determination of the permanence and extinction of the species x in the patch environment. We can choose appropriate diffusion rates causing system (1) either to be permanent or go extinct. The arguments here can be used to aid in a discussion of the evolution of dispersal rates.

3. STABILITY OF POSITIVE PERIODIC SOLUTION

THEOREM 4. *Suppose that Assumptions (H1) or (H2) holds, then system (1) has at least one positive ω-periodic solution that lies in $\Omega = \{(x_1, x_2, \ldots, x_n) \mid m \leq x_i \leq M, \ i = 1, 2, \ldots, n\}$.*

PROOF. By Theorems 1 and 2, any solution of (1) with positive initial values ultimately enters the region Ω, applying Theorem 2 of [9] to assert the existence of positive ω-periodic solution of (1).

Let $x^*(t) = (x_1^*(t), x_2^*(t), \ldots, x_n^*(t))$ be a positive ω-periodic solution of (1), now we consider its uniqueness and stability. This treatment incorporates prior results of the book [10] into the present argument. We introduce the following definitions.

DEFINITION 1. *An operator $U : D \subset R^n \to R^n$ is said to be monotonic if $X_1 = (x_{11}, x_{21}, \ldots, x_{n1}) \in D$, $X_2 = (x_{12}, x_{22}, \ldots, x_{n2}) \in D$, and $X_1 < X_2$ in the sense $x_{11} < x_{12}, x_{21} < x_{22}, \ldots, x_{n1} < x_{n2}$ implies $UX_1 < UX_2$.*

DEFINITION 2. *An operator $U : D \subset R^n \to R^n$ is said to be positive with respect to a cone K in R^n if $U : K \to K$, and is said be strictly positive if $UK \subset$ interior of K.*

DEFINITION 3. *An operator U defined on a cone K in R^n is said to be strongly concave, if for an arbitrary interior element $X \in K$ and any number $\tau \in (0,1)$ there exists a positive number η such that*

$$U(\tau X) \geq (1 + \eta)\tau U X.$$

Define a shift operator $A : R_+^n \to R_+^n$ by the formula

$$Ax_0 = x(\omega, x_0), \tag{15}$$

where $x(t, x_0) = (x_1(t, x_0), x_2(t, x_0), \dots, x_n(t, x_0))$ is the solution of (1) with $x(0, x_0) = x_0 = (x_{10}, x_{20}, \dots, x_{n0})$, ω denotes the period of the periodic functions $a_i(t)$, $b_i(t)$, and $D_{ij}(t)$.

THEOREM 5. *Suppose that Assumptions (H1) or (H2) holds. Then the shift operator A corresponding to (1) is monotonic, strictly positive, and strictly concave with respect to the cone R_+^n. Moreover, operator A has unique fixed point in R_+^n and the corresponding positive periodic solution is globally asymptotically stable.*

PROOF. We rewrite system (1) in the form

$$\dot{x}_i = f_i(t, x_1, x_2, \dots, x_n), \qquad i = 1, 2, \dots, n,$$

then

$$f_i(t, x_1, \dots, x_{i-1}, 0, x_{i+1}, \dots, x_n) = \sum_{j=1}^{n} D_{ij}(t) x_j \geq 0, \qquad \text{for } x_j \geq 0.$$

In addition, the functions F_i defined by

$$F_i(t, x_1, x_2, \dots, x_n) = f_i(t, x_1, x_2, \dots, x_n) - \sum_{j=1}^{n} x_j \frac{\partial f_i}{\partial x_j} = a_i(t) x_i^2(t)$$

are strictly positive in the sense that $F_i(t, x_1, x_2, \dots, x_n) > 0$ for $x_i > 0$ ($i = 1, 2, \dots, n$) and $t \geq 0$. Thus, the shift operator A is monotonic, strongly positive, and strongly concave, follows from Theorem 10.2 and Lemma 4.1 of [10].

Moreover, it is known by Theorem 10.1 of [10] and Theorem 4 of our present paper that operator A has exactly one positive fixed point in R_+^n, and hence, the periodic solution $x^*(t)$ corresponding to the fixed point of A is unique. The globally asymptotically stability of $x^*(t)$ follows from the Theorem 10.6 of [10] and $\lim_{t \to \infty} x(t) = x^*(t)$ for every solution of (1) with $x(0) \in R_+^n \setminus (0, 0)$ [10, pp. 213]. This completes the proof.

4. DISCUSSION

Takeuchi [4] showed that in a general autonomous system composed of several patches connected by diffusion and occupied by a single species, if the species is able to survive at a globally stable equilibrium point when the patches are isolated, then it continues to do so for any diffusion rate at a different equilibrium. Mahbuba and Chen [1] obtained the similar result as [4] for system (1), for any diffusion rate $D_{ij}(t) > 0$ ($i \neq j$), system (1) possesses a unique positive periodic solution that is globally asymptotically stable under the assumption that $b_i(t) > 0$ ($i = 1, 2$), this ensures that the corresponding system without diffusion ($D_{ij}(t) = 0, i, j = 1, 2$) has a unique globally asymptotically stable positive periodic solution.

Different from the above consideration, this paper focus on the more interesting cases in biology, that the species living in a weak environment in the sense that species x in some of the isolated patches will be extinct without the contribution from other patches. Dispersal can make the species x either permanent or distinct in every patch depending on the choice of the diffusion rates.

For example in Remark 4, if the patches are isolated from each other, then species x will be permanent in patch 1 and extinct in patch 2. If we restrict the diffusion rate from patch 2 to patch 1 small enough, that satisfies $[D_{12}] < 1$ or the diffusion coefficients varying in the narrow region $1/4 < [D_{12}(t) - D_{21}(t)]$ and $D_{12}(t) - D_{21}(t) \leq 5/8$, then the species x will maintain permanence in the sense that there exists a unique globally asymptotically stable positive periodic solution. This implies that dispersal increases the degree of stability of the system.

Another interesting example emerges from Remark 6, the death rate of species x in patch 2 is larger than that in the above example. If the dispersal coefficients vary in the narrow region $1 < [D_{12}(t) - D_{21}(t)]$, $D_{12}(t) - D_{21}(t) \leq 3/2$, then species x cannot survive in any patch. This implies that dispersal does not always increase population stability. If population density strongly suppresses birth rate $(b_2(t) = -2 + (1/4)\sin t)$, obligate individuals dispersal $([D_{12}(t) - D_{21}(t)] > 1)$ can actually reduce stability. On the other hand, small dispersal from patch 2 to patch 1 actually causes species x to be permanent provided that $[D_{12}] < 1$. Hence, dispersal plays an important role on the weakly population system, it can make the species either permanent or distinct by the appropriate choice of the diffusion rates.

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