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The Effect of Dispersal on Population Growth with Stage-Structure

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Abstract—Declines in species richness or population are primarily attributed to habitat destruction and fragmentation. Can we avoid the local extinction of species with stage-structure in some patches by building some corridors between the patches and controlling the dispersal rates? A conservation strategy is put forward by introducing and analyzing the asymptotic behavior of some autonomous and time-varying population models. Biological implications of these results are discussed briefly.

1. INTRODUCTION

In order to understand the effect of dispersal on the permanence and extinction of some species, the familiar dispersal model of Kolmogorov type

$$\dot{x}_i = x_i f_i(t, x_i) + \sum_{\substack{j=1 \\ j \neq i}}^{n} D_{ij}(t)\,(x_j - x_i), \qquad (i, j = 1, 2, \dots, n) \tag{1}$$

has been well studied [1–9].

In the natural world, however, there are many species whose individual members have a life history that takes them through two stages, immature and mature. In particular, we have in mind mammalian populations and some amphibious animals, which exhibit these two stages. These species do not seem to be usefully modeled by system (1). Some authors have focused their attention on the permanence and stability of some autonomous stage-structure population models with or without time delays [10–13].

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Recently, Wang and others [14] studied the living habits and characteristics of the *rana chensinensis*. *Rana chensinensis*, distributed mainly in the north and east of China, particularly in Jilin, is a well-known rare species that has important medical value. Normally, the adults of *rana chensinensis* live in forests, and they migrate to water fields for reproduction. However, water fields or moist habitats are necessary for the young *rana chensinensis* growing into mature individuals.

Because of the ecological effects of the human activities and industry, e.g., the location of manufacturing industries, the pollution of rivers, soil, etc., more and more living habitats of *rana chensinensis* were broken into patches and the breeding areas were damaged in some of these patches. Finally, in these patches, the adults of *rana chensinensis* will become extinct without contributions from other patches. In fact, many endangered and rare species—Chinese sturgeon [15], alligator sinensis [16], nipponia nippon [17], for example, face analogous problems because of the destruction and fragmentation of their habitats. In order to protect these species, we put forward the following problem.

Can we avoid the local extinction of species in some patches by building some corridors between the patches and controlling the dispersal rates?

In this paper, we try to solve this problem through advancing and analyzing some stage-structure population models.

The organization of this paper is as follows. In the next section, we introduce some models, agree on some notations, and state three lemmas which will be essential to our proofs and discussions. In Section 3, we analyze the effect of dispersal on the autonomous system (2) of single species growth with stage structure. The autonomous system corresponds to the dynamics of the species in a temporally uniform environment. We find that dispersal can make the species permanent, though it may become extinct in one patch without the contribution from other patches. In Section 4, we consider the effect of dispersal on the nonautonomous system (4) which corresponds to the dynamics of the species in a temporally nonuniform environment. Under some conditions, we show that the number of species changes periodically. Finally, the biological meaning of the results obtained in this paper are discussed briefly in Section 5.

2. MODELS AND PRELIMINARIES

To solve the problem that was put forward in Section 1, we suppose that the ecosystem is composed of two isolated patches and occupied by a single species whose individual members have a life history that takes them through two stages, immature and mature. Further, the breeding areas are damaged in Patch 2. Let $I_i(t)$ and $M_i(t)(i = 1, 2)$ denote the density of immature and mature populations in the i^{th} patch, respectively. Let $I_1(0)$, $M_1(0)$, and $M_2(0)$ be the observed value of $I_i(t)$, $M_1(t)$, and $M_2(t)$ at initial time $t = 0$, respectively. To derive our model equations, we make the following assumptions.

HYPOTHESIS H1. The birth rate into the immature population in Patch 1 is proportional to the existing mature population with proportionality constant a.

HYPOTHESIS H2. The death rate of the immature population in Patch 1 is proportional both to the existing immature population and to the square of it with proportionality constants c and b, respectively.

HYPOTHESIS H3. The death rate of the mature population in the i^{th} patch is of a logistic nature, i.e., proportional to the square of the population with proportionality constant $\beta_i > 0$, $i = 1, 2$.

HYPOTHESIS H4. The rate of transition from immature individuals to mature individuals is proportional to the existing immature population with proportionality constant α (see [12,13]).

Under the above assumptions, we propose a model to describe the growth of a single species population living in an isolated two patch environments where individual members of the population have a two-stage structure as follows:

$$\begin{aligned} \dot{I}_1(t) &= aM_1(t) - bI_1^2(t) - cI_1(t) - \alpha I_1(t), \\ \dot{M}_1(t) &= \alpha I_1(t) - \beta_1 M_1^2(t), \\ \dot{M}_2(t) &= -\beta_2 M_2^2(t). \end{aligned} \tag{2}$$

Obviously, $M_2(t) \to 0$ as $t \to \infty$.

If we build some corridors between the two patches, then the mature individuals can move from one patch to another.

Assume further, the following.

HYPOTHESIS H5. The net exchange of the mature population from Patch j to Patch i is proportional to the difference of the concentrations $M_j(t) - M_i(t)$ with proportionality constants $D_{ij} \geq 0$, $i, j = 1, 2$, $i \neq j$.

The dispersal model of single species growth with stage structure now are given by the follow equations:

$$\begin{aligned} \dot{I}_1(t) &= aM_1(t) - bI_1^2(t) - cI_1(t) - \alpha I_1(t), \\ \dot{M}_1(t) &= \alpha I_1(t) - \beta_1 M_1^2(t) + D_{12}\left(M_2(t) - M_1(t)\right), \\ \dot{M}_2(t) &= -\beta_2 M_2^2(t) + D_{21}\left(M_1(t) - M_2(t)\right). \end{aligned} \tag{3}$$

If the population's physical environment fluctuates periodically, then the coefficients in systems (2) and (3) are all positive and periodic functions with common period ω. Hence, we obtain the following systems (4) and (5) that correspond to systems (2) and (3), respectively.

$$\begin{aligned} \dot{I}_1(t) &= a(t)M_1(t) - b(t)I_1^2(t) - c(t)I_1(t) - \alpha(t)I_1(t), \\ \dot{M}_1(t) &= \alpha(t)I_1(t) - \beta_1(t)M_1^2(t), \\ \dot{M}_2(t) &= -\beta_2(t)M_2^2(t). \end{aligned} \tag{4}$$

$$\begin{aligned} \dot{I}_1(t) &= a(t)M_1(t) - b(t)I_1^2(t) - c(t)I_1(t) - \alpha(t)I_1(t), \\ \dot{M}_1(t) &= \alpha(t)I_1(t) - \beta_1(t)M_1^2(t) + D_{12}(t)\left(M_2(t) - M_1(t)\right), \\ \dot{M}_2(t) &= -\beta_2(t)M_2^2(t) + D_{21}(t)\left(M_1(t) - M_2(t)\right). \end{aligned} \tag{5}$$

Throughout this paper, we assume that these functions $a(t)$, $b(t)$, $c(t)$, $\alpha(t)$, $\beta_1(t)$, $\beta_2(t)$, $D_{12}(t)$, and $D_{21}(t)$ are all positive and continuous periodic functions with common period ω. To simplify our writing, we introduce the following notations: if $f(t)$ is a continuous ω-periodic function defined on $[0, \infty)$, we set

$$A_\omega(f) = \omega^{-1} \int_0^\omega f(t)\,dt, \qquad f^M = \max_t f(t), \quad f^L = \min_t f(t).$$

To prove the main results of this paper, we need the following lemmas.

LEMMA 1. *(See [5,18].) If the cooperative system*

$$\dot{x}_i = H_i(x), \quad H_i(0) = 0, \qquad i = 1, \dots, n \tag{6}$$

has the following three properties:

(i) *$DH(x)$ is irreducible for any $x \geq 0$,*
(ii) *$DH(x) \leq DH(y)$ for any $x \geq y \geq 0$,*
(iii) *all solutions are bounded,*

where $DH(x)$ is the variational matrix of $\dot{x}_i = H_i(x)$, $H_i(0) = 0$, $i = 1, \ldots, n$, then either the origin is globally stable or else there exists a unique positive equilibrium and all the trajectories in $R^n_+ \setminus \{0\}$ tend to it.

The above result can be found in [5,18].

DEFINITION. *Let $A = (a_{ij})_{n\times n}$ be an $n \times n$ matrix, and let $P_1, \ldots, P_n$ be distinct points of the complex plane. For each nonzero element a_{ij} of A, connect P_i to P_j with a directed line $\overrightarrow{P_iP_j}$. The resulting figure in the complex plane is a directed graph for A. We say that a directed graph is strongly connected if, for each pair of nodes P_i, P_j with $i \neq j$, there is a directed path*

$$\overrightarrow{P_iP_{k_1}}, \overrightarrow{P_{k_1}P_{k_2}}, \ldots, \overrightarrow{P_{k_{r-1}}P_j}$$

connecting P_i to P_j. Here, the path consists of r directed lines.

LEMMA 2. *(See [19].) A square matrix is irreducible if and only if its directed graph is strongly connected.*

LEMMA 3. *If*

$$D^M_{12}\left(c^M + \alpha^M\right) - a^L\alpha^L < 0, \tag{7}$$

then the system

$$\begin{aligned} \dot{I}_1(t) &= a^L M_1(t) - b^M I_1^2(t) - c^M I_1(t) - \alpha^M I_1(t) = P, \\ \dot{M}_1(t) &= \alpha^L I_1(t) - \beta^M M_1^2(t) - D^M_{12} M_1(t) = Q \end{aligned} \tag{8}$$

has a unique positive equilibrium, which is globally asymptotically stable.

PROOF. The equilibria for system (8) are determined by setting $\dot{I}_1(t) = \dot{M}_1(t) = 0$ and solving the intersection points of the parabola $s : a^L M_1 = b^M I_1^2 + (c^M + \alpha^M) I_1$ with parabola $l : \alpha^L I_1 = \beta^M M_1^2 + D^M_{12} M_1$. Under assumption (7), the tangent slope of l at $O(0,0)$ is larger than that of s at the same point, hence, (8) has two equilibria, $O(0,0)$ and $E(I_1^*, M_1^*)$, where I_1^* and M_1^* are positive constants. By checking the characteristic roots of (8) at $O(0,0)$ and $E(I_1^*, M_1^*)$, we know that $O(0,0)$ is unstable and $E(I_1^*, M_1^*)$ is asymptotically stable. Next we want to construct an outer boundary of a positively invariant region which contains $E(I_1^*, M_1^*)$.

Let AB and BC be the line segments of $L_1 : M_1 = q$ and $L_2 : I_1 = p$, respectively, where $A(0,q), B(p,q)$, and $C(p,0)$, and p, q are any positive constants such that

$$p > I_1^*, \frac{-D^M_{12} + \sqrt{\left(D^M_{12}\right)^2 + 4\alpha^L\beta^M p}}{2\beta^M} < q < \frac{p\left(b^M p + c^M + \alpha^M\right)}{a^L}.$$

Since

$$\dot{M}_1\Big|_{\mathrm{AB}} = \alpha^L I_1 - \beta^M q^2 - D^M_{12} q\Big|_{0\le I_1\le p} < 0$$

and

$$\dot{I}_1\Big|_{\mathrm{BC}} = a^L M_1 - b^M p^2 - \left(c^M + \alpha^M\right) p\Big|_{0\le M_1\le q} < 0,$$

AB and BC are transversals of (8). Obviously, OA and OC are also transversals of (8), and any trajectory that intersects the rectangle OABC crosses from its exterior to interior as shown in Figure 1.

Note that

$$\frac{\partial P}{\partial I_1} + \frac{\partial Q}{\partial M_1} = -2b^M I_1 - 2\beta^M M_1 - c^M - \alpha^M - D^M_{12} < 0, \qquad \text{for } (I_1, M_1) \in R^2_+,$$

the Bendixson criterion (see Edelstein-keshet [20]) holds and there are no limit cycles in R^2_+. Global stability follows from the Poincaré-Bendixson Theorem. This completes the proof.

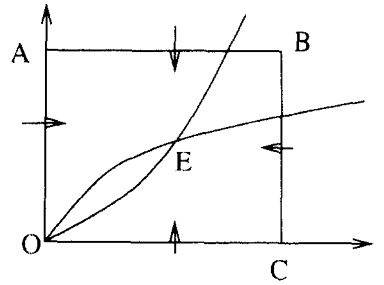

Figure 1. All trajectories which intersect the boundary OABC from exterior to interior.

LEMMA 4.. *(See [21].) Let $x(t)$ and $y(t)$ be solutions of*

$$\dot{x} = F(t, x)$$

and

$$\dot{y} = G(t, y),$$

respectively, where both systems are assumed to have the uniqueness property for initial value problems. Assume both $x(t)$ and $y(t)$ belong to a domain $D \sqsubseteq R^n$ for $[t_0, t_1]$ in which one of the two systems is cooperative and

$$F(t, z) \leq G(t, z), \qquad (t, z) \in [t_0, t_1] \times D.$$

If $x(t_0) \leq y(t_0)$, then $x(t_1) \leq y(t_1)$. If $F = G$ and $x(t_0) < y(t_0)$, then $x(t_1) < y(t_1)$.

The above result can be found in [21].

LEMMA 5. *(See [22].) Suppose that a continuous operator U maps a closed bounded convex set $\Omega \subset R^n$ into itself. Then Ω contains at least one fixed point of U; that is there exists at least one $z \in \Omega$ for which $Uz = z$ holds.*

3. EFFECT OF DISPERSAL ON SPECIES OBEYING SYSTEM (2)

In this section, we consider the asymptotic behavior of systems (2) and (3), respectively. Further, we analyze the effect of dispersal on the permanence of the species.

3.1. Without Dispersal

Obviously, $M_2(t) \to 0$ as $t \to \infty$ in (2). To analyze the asymptotic behavior of (2), we need only to consider its subsystem

$$\begin{aligned} \dot{I}_1(t) &= aM_1(t) - bI_1^2(t) - cI_1(t) - \alpha I_1(t), \\ \dot{M}_1(t) &= \alpha I_1(t) - \beta_1 M_1^2(t). \end{aligned} \tag{9}$$

Similar to the proof of Lemma 3, we obtain following result.

THEOREM 1. *System (9) has a unique positive equilibrium which is globally asymptotically stable.*

3.2. With Dispersal

THEOREM 2. *System (3) has a unique positive equilibrium and all the trajectories in $R_+^3 \setminus \{O\}$ tend to it.*

PROOF. To prove this theorem, we need only to show that (3) satisfies the assumptions of Lemma 1 and that the origin is unstable. The variational matrix of (3) takes the form

$$DH(I_1, M_1, M_2) = \begin{bmatrix} -c-\alpha-2bI_1 & a & 0 \\ \alpha & -(D_{12}+2\beta_1 M_1) & D_{12} \\ 0 & D_{21} & -(2\beta_2 M_2 + D_{21}) \end{bmatrix}.$$

By Lemma 2, $DH(I_1, M_1, M_2)$ is irreducible. For any $x \geq y \geq 0$, $DH(x) \leq DH(y)$ is obviously satisfied. The characteristic equation of $DH(I_1, M_1, M_2)$ at $O(0,0,0)$ is

$$\lambda^3 + (c+\alpha+D_{12}+D_{21})\lambda^2 + [(c+\alpha)(D_{12}+D_{21}) - a\alpha]\lambda - a\alpha D_{21} = 0. \tag{10}$$

Cubic equation (10) has at least one positive root, and so $O(0,0,0)$ is unstable.

Now we consider the boundedness of the positive solution of system (3). Choose the function

$$\rho(t) = I_1(t) + M_1(t) + M_2(t)$$

and calculate the derivative of $\rho(t)$ along solutions of (3), we have

$$\dot{\rho} = -cI_1 + (a + D_{21} - D_{12}) M_1 + (D_{12} - D_{21}) M_2 - bI_1^2 - \beta_1 M_1^2 - \beta_2 M_2^2.$$

For a positive constant ϵ ($\epsilon < c$), we have

$$\dot{\rho} + \epsilon\rho \leq (c-\epsilon)I_1 + |a + D_{21} - D_{12} + \epsilon| M_1 + |D_{12} - D_{21} + \epsilon| M_2 - bI_1^2 - \beta_1 M_1^2 - \beta_2 M_2^2.$$

Because b, β_1, and β_2 are all positive constants, there exists a positive number c_1 such that

$$\dot{\rho} + \epsilon\rho < c_1.$$

Further,

$$\rho(t) < \frac{c_1}{\epsilon} + \left(\rho(0) - \frac{c_1}{\epsilon}\right) e^{-\epsilon t}.$$

Here we obtain the boundedness of the positive solutions of system (3). This completes the proof of Lemma 1.

By Theorems 1 and 2, we can avoid the local extinction of species in Patch 2 by building some corridors between Patch 1 and Patch 2 and controlling the dispersal rates.

4. EFFECT OF DISPERSAL ON SPECIES OBEYING SYSTEM (4)

4.1. Without Dispersal

Obviously, $M_2(t) \to 0$ as $t \to \infty$ in system (4). To analyze the asymptotic behavior of (4), we need only to consider its subsystem

$$\begin{aligned} \dot{I}_1(t) &= a(t)M_1(t) - b(t)I_1^2(t) - c(t)I_1(t) - \alpha(t)I_1(t) = f_1(t, I_1, M_1), \\ \dot{M}_1(t) &= \alpha(t)I_1(t) - \beta_1(t)M_1^2(t) = f_2(t, I_1, M_1). \end{aligned} \tag{11}$$

THEOREM 3. *There exist positive constants p_1, p_2, q_1, and q_2 ($p_1 < p_2$, $q_1 < q_2$) such that the solution of (11) with positive initial values ultimately enter the rectangular region $\Omega_1 = \{(I_1, M_1) \mid p_1 \leq I_1 \leq p_2,\ q_1 \leq M_1 \leq q_2\}$, and hence, the population is permanent.*

PROOF. Obviously, R_+^2 is positively invariant with respect to system (11). For any positive solution $(I_1(t), M_1(t))$ of (11), we have

$$\begin{aligned} \dot{I}_1(t) &\geq a^L M_1(t) - b^M I_1^2(t) - c^M I_1(t) - \alpha^M I_1(t), \\ \dot{M}_1(t) &\geq \alpha^L I_1(t) - \beta_1^M M_1^2(t), \end{aligned}$$

and

$$\dot{I}_1(t) \le a^M M_1(t) - b^L I_1^2(t) - c^L I_1(t) - \alpha^L I_1(t),$$
$$\dot{M}_1(t) \le \alpha^M I_1(t) - \beta_1^L M_1^2(t).$$

By Theorem 1, the following systems

$$\begin{aligned} \dot{I}_1(t) &= a^L M_1(t) - b^M I_1^2(t) - c^M I_1(t) - \alpha^M I_1(t), \\ \dot{M}_1(t) &= \alpha^L I_1(t) - \beta_1^M M_1^2(t) \end{aligned} \tag{12}$$

and

$$\begin{aligned} \dot{I}_1(t) &= a^M M_1(t) - b^L I_1^2(t) - c^L I_1(t) - \alpha^L I_1(t), \\ \dot{M}_1(t) &= \alpha^M I_1(t) - \beta_1^L M_1^2(t) \end{aligned} \tag{13}$$

have globally stable positive equilibria $E_1(\bar{I}_1, \bar{M}_1)$ and $E_2(\tilde{I}_1, \tilde{M}_1)$, respectively.

Next we want to construct a positively invariant region for system (11).

Let $A_1(p_1, q_2)$, $B_1(p_2, q_2)$, $C_1(p_2, q_1)$, $D_1(p_1, q_1)$ be the four vertices of a rectangle $A_1B_1C_1D_1$, where p_1, p_2, q_1, and q_2 are positive constants satisfying

$$p_1 < \min\left\{\bar{I}_1, \tilde{I}_1\right\}, \frac{p_1\left(b^M p_1 + c^M + \alpha^M\right)}{a^L} < q_1 < \min\left\{\sqrt{\frac{\alpha^L p_1}{\beta_1^M}}, \bar{M}_1, \tilde{M}_1\right\},$$

$$p_2 > \max\left\{\bar{I}_1, \tilde{I}_1\right\} \text{ and } \max\left\{\sqrt{\frac{\alpha^M p_2}{\beta_1^L}}, \bar{M}_1, \tilde{M}_1\right\} < q_2 < \frac{p_2\left(b^L p_2 + c^L + \alpha^L\right)}{a^M}.$$

Since

$$\begin{aligned} \dot{M}_1|_{A_1B_1} &\le \alpha^M I_1 - \beta_1^L M_1^2\big|_{A_1B_1} \\ &= \alpha^M I_1 - \beta_1^L q_2^2\big|_{p_1 \le I_1 \le p_2} \\ &< 0, \\ \dot{I}_1|B_1C_1 &\le a^M M_1 - b^L I_1^2 - \left(c^L + \alpha^L\right) I_1\big|_{B_1C_1} \\ &= a^M M_1 - b^L p_2^2 - \left(c^L + \alpha^L\right) p_2\big|_{q_1 \le M_1 \le q_2} \\ &< 0, \\ \dot{M}_1|_{C_1D_1} &\ge \alpha^L I_1 - \beta_1^M M_1^2\big|_{C_1D_1} \\ &\ge \alpha^L p_1 - \beta_1^M q_1^2 \\ &> 0, \end{aligned}$$

and

$$\begin{aligned} \dot{I}_1|_{D_1A_1} &\ge a^L M_1 - b^M I_1^2 - \left(c^M + \alpha^M\right) I_1\big|_{D_1A_1} \\ &\ge a^L q_1 - b^M p_1^2 - \left(c^M + \alpha^M\right) p_1 \\ &> 0, \end{aligned}$$

any trajectory that intersects the rectangle $A_1B_1C_1D_1$ crosses from its exterior to interior. So the set $\Omega_1 = \{(I_1, M_1) \mid (I_1, M_1) \in A_1B_1C_1D_1\}$ is positively invariant with respect to system (11). Ω_1 lies in the interior of the nonnegative cone $R_+^2 = \{(I_1, M_1) \mid I_1 \ge 0,\ M_1 \ge 0\}$.

By the choice of the constants p_1, p_2, q_1, and q_2, the equilibra $E_1(\bar{I}_1, \bar{M}_1)$ and $E_2(\tilde{I}_1, \tilde{M}_1)$ are located in the interior of the rectangle $A_1B_1C_1D_1$. By Lemma 4 and the global stability of E_1 and E_2 with respect to R_+^2, for any positive solution of (11) with positive initial condition, there exists positive constant $T = T(I_1(0), M_1(0))$ such that $(I_1(t), M_1(t)) \in \Omega_1$ for $t \ge T$. Hence, the population is permanent. This completes the proof.

Next we consider the existence of positive periodic solution of (11) and its global stability.

Let us consider system (11) in R^2 with the norm in R^2 being defined by

$$\|(I_1, M_1)\| = \max\{|I_1|, |M_1|\}, \qquad (I_1, M_1) \in R^2.$$

We know that there exists a unique solution of (11) corresponding to every initial value $X_0 = (I_1(0), M_1(0)) = (I_1(0, X_0), M_1(0, X_0)) \in R^2_+$; let such a solution be denoted by

$$X(t, X_0) = (I_1(t, X_0), M_1(t, X_0)), \qquad t > 0,$$
$$X(0, X_0) = X_0.$$

We define a Poincaré period mapping $\mathcal{A} : R^2 \to R^2$ by the formula

$$\mathcal{A}X_0 = X(\omega, X_0).$$

If we can show that the operator $\mathcal{A}$ has a fixed point, then the periodic system (11) exists an ω-periodic solution.

THEOREM 4. *System (11) has a unique positive ω-periodic solution which is globally asymptotically stable.*

PROOF. Consider the set Ω_1 that defined in Theorem 3. Ω_1 is a bounded, closed, and convex set in the interior of R^2_+ and the operator $\mathcal{A}$ maps Ω_1 into itself, since Ω_1 is positively invariant with respect to (11), this means that

$$X^0 = (I_1^0, M_1^0) \in \Omega_1 \Longrightarrow (I_1(t, X^0), M_1(t, X^0)) \in \Omega_1,$$

for all $t \geq 0$, and hence, $(I_1(\omega, X^0), M_1(\omega, X^0)) \in \Omega_1$, which implies that $\mathcal{A}\Omega_1 \subset \Omega_1$. The solution of (11) is continuous function of their initial values, from which the continuity of the operator $\mathcal{A}$ follows. Now, by Lemma 5, the existence of at least one fixed point of $\mathcal{A}$ in Ω_1 follows. Since such a fixed point has positive coordinates, the corresponding ω-periodic solution $(I_1^*(t),\ M_1^*(t))$ is strictly positive by the positive invariance of Ω_1.

Now we consider its uniqueness and stability.

$$f_1(t, 0, M_1) = a(t)M_1 > 0, \qquad \text{for } M_1 > 0,$$
$$f_2(t, I_1, 0) = \alpha(t)I_1 > 0, \qquad \text{for } I_1 > 0.$$

The functions $F_i\ (i = 1, 2)$ defined by

$$F_1(t, I_1, M_1) = f_1(t, I_1, M_1) - I_1\frac{\partial f_1}{\partial I_1} - M_1\frac{\partial f_1}{\partial M_1} = b(t)I_1^2$$

and

$$F_2(t, I_1, M_1) = f_2(t, I_1, M_1) - I_1\frac{\partial f_2}{\partial I_1} - M_1\frac{\partial f_2}{\partial M_1} = \beta_1(t)M_1^2$$

are strictly positive for $M_1 > 0$, $I_1 > 0$, and $t \geq 0$. Thus, the operator $\mathcal{A}$ is monotonic, strongly positive and strongly concave follows from Theorem 10.2 and Lemma 10.1 of [22].

Moreover, it is known by Theorem 10.1 of [22] that operator $\mathcal{A}$ has exactly one positive fixed point in R^2_+, and hence, the periodic solution $(I_1^*(t), M_1^*(t))$ corresponding to the fixed point of $\mathcal{A}$ is unique. The globally asymptotically stability of $(I_1^*(t), M_1^*(t))$ follows from Theorem 10.6 of [22] and $\lim_{t\to\infty}(I_1(t), M_1(t)) = (I_1^*(t), M_1^*(t))$ for every solution of (11) with $(I_1(0), M_1(0)) \in R^2_+\backslash(0, 0)$ [22, p. 213]. This completes the proof.

4.2. With Dispersal

THEOREM 5. *If $D_{12}^M(c^M+\alpha^M)-a^L\alpha^L<0$, then there exist positive constants n and N $(n<N)$ such that the solution of (5) with positive initial values ultimately enters the rectangular region $\Omega_2=\{(I_1,M_1,M_2)\mid n\le I_1,M_1,M_2\le N\}$, and hence, the population is permanent.*

PROOF. Obviously, $R_+^3=\{(I_1,M_1,M_2)\mid I_1\ge 0,\ M_1\ge 0,\ M_2\ge 0\}$ is positively invariant with respect to system (5). Suppose $(I_1(t),M_1(t),M_2(t))$ is a positive solution of (5). Then we have

$$\dot I_1(t)\ge a^LM_1(t)-b^MI_1^2(t)-\left(c^M+\alpha^M\right)I_1(t),$$
$$\dot M_1(t)\ge \alpha^LI_1(t)-\beta_1^MM_1^2(t)-D_{12}^MM_1(t).$$

By the results of Lemmas 3 and 4, there exist positive constants I_1^0 and M_1^0 such that

$$\lim_{t\to\infty}\inf I_1(t)\ge I_1^0,\qquad \lim_{t\to\infty}\inf M_1(t)\ge M_1^0.$$

Further, for every given $\epsilon>0\,(\epsilon<M_1^0)$, there exists $T_0=T_0(I_1(0),M_1(0))>0$ such that

$$\dot M_2\ge -\beta_2^MM_2^2-D_{21}^MM_2+D_{21}^L\left(M_1^0-\epsilon\right)=f\left(M_2\right),$$

for all $t>T_0$. The algebraic equation

$$\beta_2^MM_2^2+D_{21}^MM_2-D_{21}^L\left(M_1^0-\epsilon\right)=0$$

gives us one positive root

$$\tilde M_2=\frac{-D_{21}^M+\sqrt{\left(D_{21}^M\right)^2+4\beta_2^MD_{21}^L\left(M_1^0-\epsilon\right)}}{2\beta_2^M}.$$

Clearly, $f(M_2)>0$ for every positive number $M_2(0\le M_2<\tilde M_2)$. Choose $M_2^0(0<M_2^0<\tilde M_2)$, $\dot M_2|_{M_2=M_2^0}\ge f(M_2^0)>0$. If $M_2(T_0)\ge M_2^0$, then it also holds for $t\ge T_0$. If $M_2(T_0)<M_2^0$, then

$$\dot M_2\left(T_0\right)\ge \inf\left\{f\left(M_2\right)\mid 0\le M_2<M_2^0\right\}>0,$$

there must exist $T_1(\ge T_0)$ such that $M_2(t)\ge M_2^0$ for $t\ge T_1$.

Next we will show that the positive solution of (5) is also ultimately bounded above. Choose the function

$$\rho(t)=I_1(t)+M_1(t)+M_2(t),$$

and calculate the derivative of $\rho(t)$ along the solution of (5), we have

$$\dot\rho+\epsilon\rho\le\left(c^L-\epsilon\right)I_1+\mid a^M+D_{21}^M-D_{12}^L+\epsilon\mid M_1+\mid D_{12}^M-D_{21}^L+\epsilon\mid M_2-b^LI_1^2-\beta_1^LM_1^2-\beta_2^LM_2^2,$$

for some positive constant $\epsilon(\epsilon<c^L)$. Because b^L, β_1^L, and β_2^L are all positive constants, there exists a positive number c_2 such that $\dot\rho+\epsilon\rho<c_2$. So

$$\rho(t)<\frac{c_2}{\epsilon}+\left(\rho(0)-\frac{c_2}{\epsilon}\right)e^{-\epsilon t}.$$

Hence, there exist positive numbers T_2 and N such that $I_1(t)$, $M_1(t)$, and $M_2(t)$ less than N for $t\ge T_2$. Denoting $T=\max\{T_1,T_2\}$, $n=\min\{I_1^0,M_1^0,M_2^0\}$, we have $n\le I_1(t),\ M_1(t),M_2(t)\le N$ for $t\ge T$. This completes the proof.

THEOREM 6. *If $D_{12}^M(c^M+\alpha^M)-a^L\alpha^L<0$, then system (5) has a unique positive ω-periodic solution which is globally asymptotically stable.*

PROOF. First, we construct a positively invariant set for system (5). From the assumption of this theorem and Lemma 3, the following system:

$$\dot I_1(t) = a^L M_1(t) - b^M I_1^2(t) - c^M I_1(t) - \alpha^M I_1(t),$$
$$\dot M_1(t) = \alpha^L I_1(t) - \beta_1^M M_1^2(t) - D_{12}^M M_1(t)$$

has a unique positive equilibrium (I_1^0, M_1^0) which is globally asymptotically stable. Choosing fixed positive constants p_3, q_3, and r_3 which satisfy

$$p_3 < I_1^0, \frac{p_3\left(b^M p_3 + c^M + \alpha^M\right)}{a^L} < q_3 < \frac{-D_{12}^M + \sqrt{\left(D_{12}^M\right)^2 + 4\alpha^L\beta_1^M p_3}}{2\beta_1^M},$$
$$r_3 < \frac{-D_{12}^M + \sqrt{\left(D_{12}^M\right)^2 + 4\beta_2^M D_{12}^L q_3}}{2\beta_2^M},$$

we define four plane regions ϕ_1, ϕ_2, ϕ_3, and ϕ_4, where $\phi_1 : I_1 = p_3(M_1 \ge q_3,\ M_2 \ge r_3)$, $\phi_2 : M_1 = q_3(I_1 \ge p_3,\ M_2 \ge r_3)$, $\phi_3 : M_2 = r_3(I_1 \ge p_3,\ M_1 \ge q_3)$, $\phi_4 : \rho = (c_2/\epsilon)$, ρ, c_2, and ϵ are defined in the proof of Theorem 5 and $(c_2/\epsilon) > p_3 + q_3 + r_3$. These planes ϕ_1, ϕ_2, ϕ_3, ϕ_4 enclose a set $\Omega_3(\subset \text{int } R_+^3)$.

Since

$$\begin{aligned}
\dot I_1 \left|\phi_1\right. &\ge a^L M_1 - b^M p_3^2 - \left(c^M + \alpha^M\right) p_3 \big| M_1 \ge q_3 \\
&> 0, \\
\dot M_1|\phi_2 &\ge \alpha^L I_1 - \beta_1^M q_3^2 - D_{12}^M q_3 | I_1 \ge p_3 \\
&\ge \beta_1^M \left(q_3 + \frac{D_{12}^M + \sqrt{\left(D_{12}^M\right)^2 + 4\alpha^L\beta_1^M p_3}}{2\beta_1^M}\right)\left(-q_3 + \frac{-D_{12}^M + \sqrt{\left(D_{12}^M\right)^2 + 4\alpha^L\beta_1^M p_3}}{2\beta_1^M}\right) \\
&> 0, \\
\dot M_2 \mid \phi_3 &\ge -\beta_2^M r_3^2 - D_{21}^M r_3 + D_{21}^L q_3 \\
&> 0.
\end{aligned}$$

From the proof of Theorem 5, there exist positive constants ϵ and c_2 such that $\dot\rho + \epsilon\rho < c_2$, we have

$$\dot\rho \mid \phi_4 < 0.$$

Then Ω_3 is positively invariant with respect to (5).

Define a Poincaré period mapping $\mathcal{B} : R_+^3 \to R_+^3$ by the formula

$$\mathcal{B}\mathrm{P}_0 = Y(\omega, P_0),$$

where $Y(t, P_0) = (I_1(t, P_0), M_1(t, P_0), M_2(t, P_0))$ is the solution of (5) with $Y(0, P_0) = P_0 = (I_1(0, P_0), M_1(0, P_0), M_2(0, P_0))$. Similar to the discussion in the proof of Theorem 4, we can obtain a fixed point in the interior of Ω_3. Since such a fixed point has positive coordinates, the corresponding ω-periodic solution $\Gamma(t) = (I_1^{**}(t), M_1^{**}(t), M_2^{**}(t))$ of (5) is strictly positive. We rewrite system (5) in the form

$$\dot I_1 = g_1(t, I_1, M_1, M_2),$$
$$\dot M_1 = g_2(t, I_1, M_1, M_2),$$
$$\dot M_2 = g_3(t, I_1, M_1, M_2).$$

Denote by $g_{ij}(t,\xi)$ the values of the function $g_i(t,\xi_1,\xi_2,\xi_3)$ for $\xi_j=\xi, \xi_k=0\,(k=1,2,3;k\neq j)$. There exists a sequence of indices $\{1,2,3,2,1\}$ such that

$$\beta(t,I_1,M_1,M_2)=g_{12}(t,M_1)\,g_{23}(t,M_2)\,g_{32}(t,M_1)\,g_{21}(t,I_1)=a(t)\alpha(t)D_{12}(t)D_{21}(t)I_1M_1^2M_2$$

is strongly positive for any t with positive I_1, M_1, and M_2. In addition, the following functions G_i defined by

$$G_1(t,I_1,M_1,M_2)=g_1(t,I_1,M_1,M_2)-I_1\frac{\partial g_1}{\partial I_1}-M_1\frac{\partial g_1}{\partial M_1}-M_2\frac{\partial g_1}{\partial M_2}=b(t)I_1^2,$$
$$G_2(t,I_1,M_1,M_2)=g_2(t,I_1,M_1,M_2)-I_1\frac{\partial g_2}{\partial I_1}-M_1\frac{\partial g_2}{\partial M_1}-M_2\frac{\partial g_2}{\partial M_2}=\beta_1(t)M_1^2,$$
$$G_3(t,I_1,M_1,M_2)=g_3(t,I_1,M_1,M_2)-I_1\frac{\partial g_3}{\partial I_1}-M_1\frac{\partial g_3}{\partial M_1}-M_2\frac{\partial g_3}{\partial M_2}=\beta_2(t)M_2^2$$

are strictly positive in the sense that $G_i(t,I_1,M_1,M_2)>0$ for all positive I_1, M_1, M_2, and $t\geq 0$. Thus, the operator $\mathcal{B}$ is monotonic, strongly positive and strongly concave follows from Theorem 10.2 and Lemma 10.2 of [22].

Moreover, it is known by Theorem 10.1 of [22] that operator $\mathcal{B}$ has exactly one positive fixed point in R_+^3, and hence, the periodic solution $\Gamma(t)$ corresponding to the fixed point of $\mathcal{B}$ is unique. The globally asymptotic stability of $\Gamma(t)$ follows from Theorem 10.6 of [22] and $\lim_{t\to\infty}(I_1(t),M_1(t),M_2(t))=(I_1^{**}(t),M_1^{**}(t),M_2^{**}(t))$ for every solution of (11) with $(I_1(0), M_1(0),M_3(0))\in R_+^3\backslash(0,0,0)$ [22, p. 213]. This completes the proof.

5. DISCUSSION

Because of the ecological effects of human activities and industry, the location of manufacturing industries, the pollution of the atmosphere, rivers, soil, etc., more and more habitats are broken into patches and some of the patches are polluted. In some of these patches, the species will become extinct without contributions from other patches, and hence, the species live in a weak patchy environment.

In this paper, we considered the effects of dispersal on the permanence of some single species models with stage structure. Within the context of these models (2)–(5) used here, the results of this paper imply that the species will become extinct in Patch 2 if the two patches are isolated from each other. But we can build some corridors between Patch 1 and Patch 2 to allow the adults species to move from one patch to another for reproduction and other behavior. By controlling the dispersal rates between the patches, we can avoid the local extinction of species in Patch 2. Hence, corridors between patches and controlling of dispersal rates play an important role on population growth.

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