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A Nonlinear Model for Migrating Species*

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We propose a nonlinear model for migrating populations based on a system of population patches. The equations are shown to have a unique global solution under realistic hypotheses. Estimates for solutions and the existence of equilibria are investigated and necessary and sufficient conditions for equilibria are given.

1. INTRODUCTION

Continuous models for population dynamics are based on the basic ideas of growth and decay, known for many years. A major change in population studies was introduced by Sharp and Lotka [3] with age structure, the total population at time t being defined by a population density function $\rho(a, t)$ dependent on both age a and time t. That is, the population $P(t)$ at time t is assumed to be given by

$$P(t) = \int_0^U \rho(a, t)\, da. \tag{1.1}$$

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Where U is the upper limit of possible age (we assume $U < \infty$). This gives the distinct and realistic advantage of allowing the death and birth processes to be age-dependent.

One process that characterizes many bio-populations is *migration*. Migration has received less attention than other population variables and few models have introduced migration into age-dependent schemes. Many bio-populations migrate from a birth location or several birth locations and then reproduce elsewhere, or return to the primary location to reproduce. To model the general case of such behavior, we have introduced and we have studied some characteristics of a seasonal linear model involving migration and age-dependence [1].

It is reasonable to assume however that birth and death processes for a population would depend on $P(t)$, the size of the population, as well as age and time [2, 4].

A natural way to approach this problem is to consider several populations residing in "patches" and migrating between these patches, allowing for the possibility of different birth and death parameters in each patch and between "natives" and "migrants" in the same patch. If we assume there are $N \geq 2$ patches, then the rate of change of native population density l_i in patch i would be given by

$$Dl_i(a,t) = \lim_{h \to 0} \frac{l_i(a+h, t+h) - l_i(a,t)}{h}. \tag{1.2}$$

This, because when time is incremented, age is incremented by an equal amount. This quantity added to the number who die or leave the patch should be zero (the so-called balance law.) A similar expression would define the rate of change for the migrant density in patch i except that here the density must depend in general on the length of time b (always less than or equal to a) spent "in patch." Hence the rate of change of migrant density m_i in patch i would be

$$Dm_i(a,b,t) = \lim_{h \to 0} \frac{m_i(a+h, b+h, t+h) - m_i(a,b,t)}{h}. \tag{1.3}$$

Once again, population balance would require that this rate, when added to death and migration factors, gives zero. The total population in patch i would then be

$$P_i(t) = \int_0^U l_i(a,t)\,da + \int_0^U \int_0^a m_i(a,b,t)\,db\,da. \tag{1.4}$$

This naturally gives rise to the notion of a "population vector" $P(t)$, the coordinates of this vector are the scalar quantities, $P_i(t)$. The population "velocity" or

$$\frac{d}{dt}P(t) = \dot{P}(t), \tag{1.5}$$

which describes the evolution of the system in terms of location, is determined by both migration rates and patch conditions.

Other important data are birth rates of patch natives and migrants to that patch (which could be different) and arrival rates of migrants to a patch. These quantities are expressed as the values of $l_i(0,t)$ and $m_i(a,0,t)$, respectively. These quantities will be defined in terms of birth and migration factors, which should in turn depend on P. They should be population age determined as well. Reasonable expressions for these requirements are

$$\begin{aligned} l_i(0,t) &= \int_0^U \beta_i(a,t,P(t))l_i(a,t)\,da \\ &\quad + \int_0^U \int_0^a \gamma_i(a,b,t,P(t))m_i(a,b,t)\,db\,da, \end{aligned} \tag{1.6}$$

$$\begin{aligned} m_i(a,0,t) &= \sum_{j \neq i} \Big[\pi_{l_{ij}}(a,t,P(t))l_j(a,t) \\ &\quad + \int_0^a \pi_{m_{ij}}(a,b,t,P(t))m_j(a,b,t)\,db \Big]. \end{aligned} \tag{1.7}$$

β_i and γ_i are called birth or fecundity coefficients, $\pi_{l_{ij}}$ and $\pi_{m_{ij}}$ are called the transfer or migration rates. With μ_{l_i} and μ_{m_i} defining death rates as multiplication operators, the two balance laws may be stated as

$$Dl_i(a,t) = -\mu_{l_i}(a,t,P)l_i(a,t) - \sum_j \pi_{l_{ji}}(a,t,P)l_i(a,t), \tag{1.8}$$

and

$$\begin{aligned} Dm_i(a,b,t) &= -\mu_{m_i}(a,b,t,P)m_i(a,b,t) \\ &\quad - \sum_j \pi_{m_{ji}}(a,b,t,P)m_i(a,b,t). \end{aligned} \tag{1.9}$$

We add the initial conditions,

$$l_i(a,0) = l_{iO}(a), \tag{1.10}$$

$$m_i(a,b,0) = m_{iO}(a,b). \tag{1.11}$$

The problems (1.7)–(1.11) are studied in detail in Section 2. We give initial hypotheses on the birth, death (for which we allow the natural singularity at $a = U$), and transfer coefficients and we state the precise setting in which solutions are to be considered. We prove that under the given conditions on the birth, death, and transfer coefficients, a unique solution exists which is "positive" in a certain sense. Because the case of time-dependent coefficients is important in examples [1], we treat the problem in this case for existence of solutions. Hypotheses sufficient for global existence are given. The functions l and m of (1.8) and (1.9) are not smooth in the classical sense, only the directional derivatives Dl and Dm are required. Estimates on the growth rate of solutions are given by treating the system in terms of certain nonlinear integral equations and existence of solutions is established by a fixed point argument using these integral equations.

In Section 3 we study the same system under the additional hypothesis that the coefficients are time-independent. Equilibrium solutions are considered. We will consider stability of equilibria, periodic solutions, and delay terms (important for fisheries, for example) elsewhere.

The present extension of the theory can be applied to a number of real species. A primary example of this is ocean fisheries. In [1] we considered the example of the saithe. Here we can extend that model to one which contains the so-called "fishing effort," a nonlinear term of the form,

$$q\left(a, t, \int_0^U j(a, t, c) k(c, P(c))\, dc\right),$$

in the death rate coefficient. The mechanisms of migration differ in a patch system depending on age, season, and other species-specific factors. Some general mechanisms that appear important are mixtures of random walk (in the case of some fish larvae) and atmospheric (ocean) conditions. We intend to discuss different types of movement as a development of the theory given here in the future.

2. EXISTENCE OF SOLUTIONS

We start by giving more precise definitions and interpretations of quantities introduced in the previous section. Then we reformulate the problems (1.7)–(1.11) as vector integral equations, an equivalent form when solutions are sufficiently regular.

DEFINITIONS 2.1. N = the number of patches. $\Omega = \{(a, b) \mid 0 \le b < a < U\}$ is a bounded subset of $\mathbf{R}^2$. $l_i(a, t)$ = population (density) in patch i

of "age" a at time t. $1 \le i \le N$. $m_i(a, b, t)$ = population (density) in patch i of migrants from other patches of age a, having lived in patch i for time b, at time t. $(b < a)$ $1 \le i \le N$. ${}^tA$ indicates the transpose of a matrix or vector A. The total population in patch i is given by, $1 \le i \le N$.

$$P_i(t) = \int_0^U l_i(a,t)\,da + \int_0^U \int_0^a m_i(a,b,t)\,db\,da.$$

The population vector is given by

$$P(t) = {}^t\left(P_1(t), P_2(t), P_3(t), \ldots, P_N(t)\right).$$

When necessary to distinguish between the populations for different densities, we shall use P with subscripts, P_{lm} to indicate population for densities l and m. $\pi_{l_{ij}}(a, t, P(t))$ = migration rate from patches j to i (in general, population dependent) of natives from patch j. This function is assumed to vanish at $a = 0$ and at $a = U$. $K \ge \pi_{l_{ij}} \ge 0$ for some K. $\pi_{l_{ij}} = 0$ when $i = j$. $\pi_{m_{ij}}(a, t, b, P)$ = migration rate from patch j to patch i (in general, population dependent) of migrants from patch j. This function is assumed to vanish at $a = 0$ and at $a = U$. $K \ge \pi_{m_{ij}} \ge 0$ for some K. $\pi_{m_{ij}} = 0$ when $i = j$. $\pi_l(a, t, P)$ = the matrix $[\pi_{l_{ij}}(a, t, P)]$, $1 \le i \le N$, $1 \le j \le N$. $\pi_m(a, b, t, P)$ = the matrix $[\pi_{m_{ij}}(a, t, b, P)]$, $1 \le i \le N$, $1 \le j \le N$. We assume π_l and π_m are uniformly (norm) bounded by some constant. $|\pi_l(a, t, P)| \le C_1$, $|\pi_m(a, b, t, P)| \le C_2$. $M(a, b, t)$ = the N-vector ${}^t(m_i(a, b, t))$. m_i: $\Omega \times (0, \infty) \to \mathbf{R}^N$. $L(a, t)$ = the N vector ${}^t(l_i(a, t))$. L: $(0, U) \times (0, \infty) \to \mathbf{R}^N$. Then the population vector, $P(t)$, is given by

$$P(t) = \int_0^U L(a,t)\,da + \int_0^U \int_0^a M(a,b,t)\,db\,da.$$

$\mu_{l_i}(a, t, P)$ = mortality rate in patch i for nonmigrants. $\mu_{l_i}(a, t, P) \ge 0$, and $\mu_{l_i}(a, t, P) \to \infty$ as $a \to U$ for each t, P. (Individuals die by age U.) $\mu_{m_i}(a, b, t, P)$ = mortality rate in patch i for migrants. $\mu_{m_i}(a, b, t, P) \ge 0$ and $\mu_{m_i}(a, b, t, P) \to \infty$ as $a \to U$ for each b, P, and t. $\Delta_{l_i}(a, t, P) = \mu_{l_i}(a, t, P) + \sum_j \pi_{ji}(a, t, P)$. $\Delta(a, t, P) = \operatorname{diag}(\Delta_{l_i}(a, t, P))$. $\Delta_{m_i}(a, b, t, P) = \mu_{m_i}(a, b, t, P) + \sum_j \pi_{ji}(a, b, t, P)$. $\Delta(a, b, t, P) = \operatorname{diag}(\Delta_{m_i}(a, b, t, P))$. $\beta_i(a, t, P)$ is the (average) fertility rate for present natives of patch i. $\gamma_i(a, b, t, P)$ is the (average) fertility rate of migrants into patch i. $B(a, t, P) = \operatorname{diag}(\beta_i(a, t, P))$, $\Gamma(a, b, t, P) = \operatorname{diag}(\gamma_i(a, b, t, P)$. We assume that B and Γ are uniformly bounded. Thus,

$$|B(a,t,P)| \le D_1, \qquad |\Gamma(a,b,t,P)| \le D_2.$$

We assume that Δ_m and Δ_l are Lipschitz in P in the following way: Assume $0 \le t \le T < \infty$, and that $a \le c < U$. Then

$$\left|\Delta_m(a,b,t,P_{lm}(t)) - \Delta_m(a,b,t,P_{l'm'}(t))\right| \le R(c)\left|P_{lm}(t) - P_{l'm'}(t)\right|.$$

A similar statement for Δ_l will be assumed. Likewise we assume a similar property for β and π, the various birth and transfer functions. Hence,

$$\begin{aligned}
l_i(a,0) &= l_{iO}(a), \qquad 0 \le a \le U,\\
L(a,0) &= L_o(a) = {}^t\left(l_{1o}(a), l_{2o}(a), \dots, l_{No}(a)\right), \qquad 0 \le a \le U,\\
m_i(a,b,0) &= m_{io}(a,b), \qquad (a,b) \in \Omega,\\
M(a,b,0) &= M_o(a,b) = {}^t\left(m_{1o}(a,b), m_{2o}(a,b), \dots, m_{No}(a,b)\right),\\
&\qquad\qquad (a,b) \in \Omega.
\end{aligned}$$

$D =$ represents the (distributional) $\mathbf{1} \circ \nabla$ operator, $\mathbf{1} = (1,1)$ or $(1,1,1)$ depending on the variable number in ∇.

DEFINITION 2.2. The space X_r is the space of all functions ${}^t(L(a,t), M(a,b,t))$ with norm,

$$|(L,M)|_{X_r} = \sup\left\{e^{-rt}\left(|L(\cdot,t)|_{L^1} + |M(\cdot,\cdot,t)|_{L^1}\right), 0 \le t \le T\right\}. \quad (2.1)$$

We define $X = X_0$.

DEFINITION 2.3. A solution to the migration problem up to time $T > 0$ is a vector-valued function ${}^t(L,M)$ on $(0,U) \times (0,T) \otimes \Omega \times (0,T)$ with the following properties:

(a) (DL, DM) exists on $(0,U) \times (0,T) \otimes \Omega \times (0,T)$ and ${}^t(L,M)$ is in $L^1((0,U) \otimes \Omega)$ for $0 \le t \le T$, with finite norm in X_r.

(b) $Dl_i(a,t) = -\mu_{l_i}(a,t,P)l_i(a,t) - \sum_j \pi_{ji}(a,t,P)l_i(a,t)$ and

$$\begin{aligned}
Dm_i(a,b,t) = {}& -\mu_{m_i}(a,b,t,P)m_i(a,b,t)\\
& - \sum_j \pi_{ji}(a,b,t,P)m_i(a,b,t),
\end{aligned}$$

for $0 < b < a$, $0 < t < T$. Hence,

$$\begin{aligned}
l_i(a,0) &= l_{iO}(a), \qquad (a \ge 0),\\
m_i(a,b,0) &= m_{iO}(a,b), \qquad (a,b) \text{ in } \Omega.
\end{aligned}$$

(c)
$$l_i(0,t) = \int_0^U \beta_i(a,t,P(t))l_i(a,t)\,da + \int_0^U\int_0^a \gamma_i(a,b,t,P(t))m_i(a,b,t)\,db\,da$$
$$m_i(a,0,t) = \sum_{j\neq i}\left[\pi_{l_{ij}}(a,t,P(t))l_j(a,t) + \int_0^a \pi_{m_{ij}}(a,b,t,P(t))m_j(a,b,t)\,db\right],$$

for $t > 0$.

The migration problem up to time T has another formulation which we now give. The definitions of L and M make it apparent that (b) and (c) are equivalent to

(d)
$$DL(a,t) = -\Delta_l(a,t)L(a,t),$$
$$DM(a,b,t) = -\Delta_m(a,b,t,P)M(a,b,t),$$
$$\text{for } 0 < b < a,\ 0 < t < T.$$
$$L(a,0) = L_O(a), \qquad (a \geq 0),$$
$$M(a,b,0) = M_O(a,b), \qquad (a,b) \text{ in } \Omega.$$

(e)
$$L(0,t) = \int_0^U B(a,t,P(t))L(a,t)\,da + \int_0^U\int_0^a \Gamma(a,b,t,P(t))M(a,b,t)\,db\,da,$$
$$M(a,0,t) = \pi_l(a,t,P(t))L(a,t) + \int_0^a \pi_m(a,b,t,P(t))M(a,b,t)\,db,$$

for $t > 0$. If L and M are solutions to (d) and (e) and $h > 0$, then

$$DL(a_o+h,t_o+h) = \frac{d}{dh}L(a_o+h,t_o+h),$$

and (∗)

$$DM(a_o+h,h,t_o+h) = \frac{d}{dh}M(a_o+h,h,t_o+h).$$

Because the Δ matrices are diagonal, it is easy to see that with a change of variables we have

$$L(a,t) = \left\{ \begin{array}{l} \exp\left(-\int_0^t \Delta_l(a-t+s, s, P_{lm}(s))\, ds \right) L_o(a-t), t < a \\ \exp\left(-\int_{t-a}^t \Delta_l(s-t+a, s, P_{lm}(s))\, ds \right) L(0, t-a), a < t \end{array} \right\}, \tag{2.2}$$

$$M(a,b,t) = \left\{ \begin{array}{l} \exp\left(-\int_0^t \Delta_m(s+a-t, s+b-t, s, P(s))\, ds \right) \\ \qquad \times M_o(a-t, b-t), t < b \\ \exp\left(-\int_{t-b}^t \Delta_m(s+a-t, s+b-t, s, P(s))\, ds \right) \\ \qquad \times M(a-b, 0, t-b), b < t \end{array} \right\}, \tag{2.3}$$

$$\begin{aligned} L(0,t) &= \int_0^U B(a,t,P(t)) L(a,t)\, da \\ &\quad + \int_0^U \int_0^a \Gamma(a,b,t,P(t)) M(a,b,t)\, db\, da, \end{aligned} \tag{2.4}$$

$$\begin{aligned} M(a,0,t) &= \pi_l(a,t,P(t)) L(a,t) \\ &\quad + \int_0^a \pi_m(a,b,t,P(t)) M(a,b,t)\, db. \end{aligned} \tag{2.5}$$

We are now able to state

THEOREM 1. *Let $^t(L, M)$ be a solution to the migration problem up to time $T > 0$. Then the solutions L and M are solutions to* (2.2)–(2.5).

To prove the converse of the theorem requires some smoothness assumptions on the coefficients which we do not wish to make. The idea would be to let L and M be solutions to (2.2)–(2.5). Make the change of variables in (2.2) and (2.3) as given in $(*)$. Equation (2.2) then becomes

$$L(a_o + h, t_o + h)$$

$$= \left\{ \begin{array}{l} \exp\left(-\int_0^{t_o+h} \Delta_l(a_o - t_o + s, s, P_{lm}(s))\, ds \right) L_o(a_o - t_o), t_o < a_o, \\ \exp\left(-\int_{t_o - a_o}^{t_o+h} \Delta_l(s - t_o + a_o, s, P_{lm}(s))\, ds \right) L(0, t_o - a_o), a_o < t_o \end{array} \right\}, \tag{2.6}$$

with a similar expression for M. It is apparent that D may now be applied to both sides of these expressions which yields (d). It is clear from (2.2) and (2.3) that discontinuities are propagated along characteristics, and that across $t = a$, or $t = b$, a solution may be discontinuous. Continuity across $t = a$ and $t = b$ can be guaranteed by requiring that L_o and M_o satisfy the compatibility conditions,

$$L_0(0) = \int_0^U B(a, 0, P(0)) L_o(a)\, da + \int_0^U \int_0^a \Gamma(a, b, 0, P(0)) M_o(a, b)\, db\, da,$$

and (2.7)

$$M_o(a, 0) = \pi_l(a, 0, P(0)) L_o(a) + \int_0^a \pi_m(a, b, 0, P(0)) M_o(a, b)\, db.$$

From (2.2) and (2.3) we see that if L_o and M_o are continuous, L and M are continuous away from $t = a$, or $t = b$, if the coefficients have sufficient continuity.

If we require the L and M have more regularity, then we must require more regularity of the coefficients in the problem, i.e., the Δ functions, B and Γ as well as L_o and M_o. In addition, other identities besides (2.7) are required. We do not pursue this here. Instead, we note we can show the existence of a solution to the "weaker" version [(2.2)–(2.5)] of the migration problem for $T > 0$. We now show that a rigorous solution to (2.2)–(2.5) exists in X. However, because boundary values like $L(a, 0)$ and $M(a, 0, t)$ do not necessarily exist in X, we must modify the system (see (2.8)–(2.11)) using (2.4) and (2.5). This is not a difficulty, because we do not use actual pointwise limits of these boundary values in the sequel. Any solution of the population problem will obey the estimates derived for our weak version.

THEOREM 2. *The system* (2.2)–(2.5) *has a unique solution in* X.

Proof. We approach the proof by means of the contraction mapping theorem. We exhibit a closed subset of a Banach space on which a certain mapping is a strict contraction. It therefore has a fixed point there, and this fixed point is the solution we desire. First, we introduce some notation. We have

$$G(a, t, P_{lm}) = M(a, 0, t) = \pi_l(a, t, P_{lm}(t)) L(a, t) + \int_0^a \pi_m(a, b, t, P_{lm}(t)) M(a, b, t)\, db, \tag{2.8}$$

$$C(t, P_{lm}) = L(0, t) = \int_0^U B(a, t, P_{lm}(t)) L(a, t)\, da + \int_0^U \int_0^a \Gamma(a, b, t, P_{lm}(t)) M(a, b, t)\, db\, da. \quad (2.9)$$

Note that the right-hand sides of G and C are defined for any M and L in X. Then

$$L(a, t) = \begin{Bmatrix} \exp\left(-\int_0^t \Delta_l(a - t + s, s, P_{lm}(s))\, ds \right) L_o(a - t), t < a, \\ \exp\left(-\int_{t-a}^t \Delta_l(s - t + a, s, P_{lm}(s))\, ds \right) C(t - a, P_{lm}(t - a)), a < t \end{Bmatrix}, \quad (2.10)$$

$$M(a, b, t) = \begin{Bmatrix} \exp\left(-\int_0^t \Delta_m(s + a - t, s + b - t, s, P_{lm}(s))\, ds \right) \\ \quad \times M_o(a - t, b - t), t < b, \\ \exp\left(-\int_{t-b}^t \Delta_m(s + a - t, s + b - t, s, P_{lm}(s))\, ds \right) \\ \quad \times G(a - b, t - b, P_{lm}(t - b)), b < t \end{Bmatrix}. \quad (2.11)$$

Define the right-hand side of (2.10) and (2.11) to be $I(L, M)$. To distinguish between population vectors for different densities, we write $P_{l'm'}$ for the population vector for a pair (L', M').

We need some *a priori* estimates on (L, M). Using (2.8)–(2.11) and somewhat tedious computations, we arrive at an estimate of the form,

$$|(L, M)|_{L^1}(t) \leq |(L_o, M_o)|_{L^1} + K \int_o^t |(L, M)|_{L^1}(s)\, ds, \quad (2.12)$$

where K is a constant depending on the bounds of B, Γ, and π_l, π_m. To construct such an estimate, we observe that by (2.10) and (2.11),

$$|(L, M)|_{L^1}(t) \leq \int_t^U \left| \exp\left(-\int_0^t \Delta_l(a - t + s, s, P_{lm}(s))\, ds \right) L_o(a - t) \right| da + \int_0^t \left| \exp\left(-\int_{t-a}^t \Delta_l(s - t + a, s, P_{lm}(s))\, ds \right) C(t - a, P_{lm}(t - a)) \right| da$$

$$+\int_t^U\int_t^a\left|\exp\left(-\int_0^t\Delta_m(s+a-t,s+b-t,s,P_{lm}(s))\,ds\right)\right.$$

$$\left.\times M_o(a-t,b-t)\right|\,db\,da$$

$$+\int_0^t\int_0^a\left|\exp\left(-\int_{t-b}^t\Delta_m(s+a-t,s+b-t,s,P_{lm}(s))\,ds\right)\right.$$

$$\left.\times\, G\big(a-b,t-b,P_{lm}(t-b)\big)\right|\,db\,da$$

$$+\int_t^U\int_0^t\left|\exp\left(-\int_{t-b}^t\Delta_m(s+a-t,s+b-t,s,P_{lm}(s))\,ds\right)\right.$$

$$\left.\times\, G\big(a-b,t-b,P_{lm}(t-b)\big)\right|\,db\,da$$

$$\leq\int_t^U|L_o(a-t)|\,da+\int_0^t\big|C\big(t-a,P_{lm}(t-a)\big)\big|\,da$$

$$+\int_t^U\int_t^a|M_o(a-t,b-t)|\,db\,da$$

$$+\int_0^t\int_0^a\big|G\big(a-b,t-b,P_{lm}(t-b)\big)\big|\,db\,da$$

$$+\int_t^U\int_0^t\big|G\big(a-b,t-b,P_{lm}(t-b)\big)\big|\,db\,da.$$

Now take, for example, the last integral in the preceding text,

$$\int_t^U\int_0^t\big|G\big(a-b,t-b,P_{lm}(t-b)\big)\big|\,db\,da$$

$$\leq\int_t^U\int_0^t\left|\pi_l(a-b,t-b,P(t-b))L(a-b,t-b)\right.$$

$$\left.+\int_0^{a-b}\pi_m(a-b,s,t-b,P(t-b))M(a-b,s,t-b)\,ds\right|\,db\,da$$

$$\leq\int_t^U\int_0^t C_1|L(a-b,t-b)|\,db\,da$$

$$+\int_t^U\int_0^t\int_0^{a-b}C_2|M(a-b,s,t-b)|\,ds\,db\,da$$

$$= \max(C_1, C_2)\left(\int_0^t \int_{t-b}^{U-b} |L(k, t-b)|\, dk\, db \right.$$
$$\left. + \int_0^t \int_{t-b}^{U-b} \int_0^k |M(k, s, t-b)|\, ds\, dk\, db \right)$$
$$\leq \max(C_1, C_2) \int_0^t |(L, M)|_{L^1}(s)\, ds.$$

The other integrals involving G and C may be estimated in a similar way. The terms involving M_o and L_o, combine for the expression $|(L_o, M_o)|_{L^1}$.

The estimate,

$$|(L, M)|_{L^1}(t) \leq |(L_o, M_o)|_{L^1} + K\int_0^t |(L, M)|_{L^1}(s)\, ds \qquad (2.13)$$

leads to a bound on $|(L, M)|_{L^1}(t)$ of the type $|(L, M)|_{L^1}(t) \leq ce^{kt}$, which holds for all t. To see this, let $y(t)$ be the right side of (2.13). Then $|(L, M)|_{L^1}(t) \leq y(t)$, and if we substitute y for $|(L, M)|_{L^1}(t)$ in the right-hand side of (2.13) we obtain

$$0 \leq y(t) \leq |(L_o, M_o)|_{L^1} + K\int_O^t y(s)\, ds. \qquad (2.14)$$

Hence, Gronwall's inequality implies that

$$|(L, M)|_{L^1}(t) \leq y(t) \leq ce^{kt}, \qquad (2.15)$$

for some c and k (c can be taken as $|(L_o, M_o)|_{L^1}$, k as K, but of course larger values of c and k may be used).

If we consider the map I, we see that it maps X_r into X_r by (2.15) but also, if we restrict to that subset of X_r determined by the inequality (2.15), then by the same computation, we get

$$|I(L, M)|_{L^1}(t)$$
$$\leq |(L_o, M_o)|_{L^1} + K\int_O^t |(L, M)|_{L^1}(s)\, ds$$
$$\leq |(L_o, M_o)|_{L^1} + K\int_O^t ce^{ks}\, ds = |(L_o, M_o)|_{L^1} + \frac{K}{k}c(e^{kt} - 1). \qquad (2.16)$$

$|(L_o, M_o)|_{L^1} \le c$ so that

$$
\begin{aligned}
|I(L, M)|_{L^1}(t) &\le c + \frac{K}{k} c(e^{kt} - 1) = c - \frac{K}{k} c + \frac{K}{k} c e^{kt} \\
&= \left(1 - \frac{K}{k}\right) c + \frac{K}{k} c e^{kt} \\
&\le \left(1 - \frac{K}{k}\right) c e^{kt} + \frac{K}{k} c e^{kt} \\
&\le c e^{kt},
\end{aligned}
\tag{2.17}
$$

for k large enough, $(k > K)$.

Thus I maps the set of functions (L, M) satisfying $|(L, M)|_{L^1}(t) \le ce^{kt}$, into itself, for c and k sufficiently large. Such a set is a closed subset of X_r (for any r). We now assume (L, M) lies in this set. We derive estimates to show that I is a strict contraction on this set in X_r, with the appropriate value of r.

$$
\begin{aligned}
&|(L, M) - (L', M')|_{L^1}(t) \\
&\quad \le (1) \int_t^U \Bigg| \exp\left(- \int_0^t \Delta_l(a - t + s, s, P_{lm}(s))\, ds \right) L_o(a - t) \\
&\qquad\qquad - \exp\left(- \int_0^t \Delta_{l'}(a - t + s, s, P_{l'm'}(s))\, ds \right) L_o(a - t) \Bigg|\, da \\
&\qquad (2) + \int_0^t \Bigg| \exp\left(- \int_{t-a}^t \Delta_l(s - t + a, s, P_{lm}(s))\, ds \right) \\
&\qquad\qquad \times C(t - a, P_{lm}(t - a)) \\
&\qquad\qquad - \exp\left(- \int_{t-a}^t \Delta_{l'}(s - t + a, s, P_{l'm'}(s))\, ds \right) \\
&\qquad\qquad\qquad \times C(t - a, P_{l'm'}(t - a)) \Bigg|\, da \\
&\qquad (3) + \int_t^U \int_t^a \Bigg| \exp\left(- \int_0^t \Delta_m(s + a - t, s + b - t, s, P_{lm}(s))\, ds \right) \\
&\qquad\qquad \times M_o(a - t, b - t) \\
&\qquad\qquad - \exp\left(- \int_0^t \Delta_m(s + a - t, s + b - t, s, P_{l'm'}(s))\, ds \right) \\
&\qquad\qquad\qquad \times M_o(a - t, b - t) \Bigg|\, db\, da
\end{aligned}
$$

$$
\begin{aligned}
(4)\ +\int_0^t\!\int_0^a \Big|&\exp\Big(-\int_{t-b}^t \Delta_m(s+a-t,s+b-t,s,P_{lm}(s))\,ds\Big)\\
&\times G(a-b,t-b,P_{lm}(t-b))\\
&-\exp\Big(-\int_{t-b}^t \Delta_m{}'(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\Big)\\
&\qquad\qquad\times G(a-b,t-b,P_{l'm'}(t-b))\Big|\,db\,da
\end{aligned}
$$

$$
\begin{aligned}
(5)\ +\int_t^U\!\int_0^t \Big|&\exp\Big(-\int_{t-b}^t \Delta_m(s+a-t,s+b-t,P_{lm}(s))\,ds\Big)\\
&\times G(a-b,t-b,P_{lm}(t-b))\\
&-\exp\Big(-\int_{t-b}^t \Delta_m{}'(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\Big)\\
&\qquad\qquad\times G(a-b,t-b,P_{l'm'}(t-b))\Big|\,db\,da.
\end{aligned}
$$

When $t > U$, then $t > a$ and $t > b$, so there are fewer terms in that case. We treat each of the five integrals (two single integrals, three double integrals) separately as problems (1)–(5). Beginning with (1), (note that to be precisely correct in the following computation, we should integrate up to $U - \varepsilon$ and we should take limits on the first and last terms as $\varepsilon \to 0$. This is because the functions Δ in the following text are not known to be integrable on the whole of $[0, U]$. In order to avoid the more complex expressions, we assume this is done.) Thus,

$$
\begin{aligned}
\int_t^U \Big|&\exp\Big(-\int_0^t \Delta_l(a-t+s,s,P_{lm}(s))\,ds\Big)L_o(a-t)\\
&-\exp\Big(-\int_0^t \Delta_{l'}(a-t+s,s,P_{l'm'}(s))\,ds\Big)L_o(a-t)\Big|\,da\\
&\le \int_t^U \Big|\Big|\int_0^t \Delta_l(a-t+s,s,P_{lm}(s))\,ds\Big|\\
&\qquad -\Big|\int_0^t \Delta_{l'}(a-t+s,s,P_{l'm'}(s))\,ds\Big|\Big|\,|L_o(a-t)|\,da\\
&\le \int_t^U \Big|\int_0^t \Delta_l(a-t+s,s,P_{lm}(s))\,ds\\
&\qquad -\int_0^t \Delta_{l'}(a-t+s,s,P_{l'm'}(s))\,ds\Big|\,|L_o(a-t)|\,da
\end{aligned}
$$

$$= \int_t^U \left| \int_0^t \Delta_l(a - t + s, s, P_{lm}(s)) \right.$$

$$\left. - \Delta_{l'}(a - t + s, s, P_{l'm'}(s))\, ds \right| |L_o(a - t)|\, da$$

$$\leq \int_t^U \int_0^t R|P_{lm}(s) - P_{l'm'}(s)|\, ds |L_o(a - t)|\, da$$

$$\leq \int_t^U \int_0^t R(|L(\cdot, s) - L'(\cdot, s)|_{L^1} + |M(\cdot, \cdot, s) - M'(\cdot, \cdot, s)|_{L^1})\, ds$$

$$\times |L_o(a - t)|\, da$$

$$\leq \int_t^U \int_0^t R(|L(\cdot, s) - L'(\cdot, s)|_{L^1} + |M(\cdot, \cdot, s) - M'(\cdot, \cdot, s)|_{L^1})$$

$$\times e^{-rs} e^{rs}\, ds |L_o(a - t)|\, da$$

$$\leq \int_t^U \int_0^t R|(L, M) - (L', M')|_{X_r} e^{rs}\, ds |L_o(a - t)|\, da$$

$$\leq \frac{e^{rt} - 1}{r} R|(L, M) - (L', M')|_{X_r} |L_o|_{L^1}$$

$$\leq \frac{e^{rt}}{r} R|(L, M) - (L', M')|_{X_r} |L_o|_{L^1}.$$

The computation for 3 is quite similar with the obviously similar estimate. We proceed with 4 which is similar to 5. Here, we assume without loss that $t < U$. We have

$$\int_0^t \int_0^a \left| \exp\left(- \int_{t-b}^t \Delta_m(s + a - t, s + b - t, s, P_{lm}(s))\, ds \right) \right.$$

$$\times G(a - b, t - b, P_{lm}(t - b))$$

$$- \exp\left(- \int_{t-b}^t \Delta_m{}'(s + a - t, s + b - t, s, P_{l'm'}(s))\, ds \right)$$

$$\left. \times G(a - b, t - b, P_{l'm'}(t - b)) \right| db\, da$$

$$= \int_0^t \int_0^a \left| \exp\left(- \int_{t-b}^t \Delta_m(s + a - t, s + b - t, s, P_{lm}(s))\, ds \right) \right.$$

$$\times G(a - b, t - b, P_{lm}(t - b))$$

$$
\begin{aligned}
&-\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\\
&\times G(a-b,t-b,P_{l'm'}(t-b))\\
&+\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\\
&\times G(a-b,t-b,P_{lm}(t-b))\\
&-\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\\
&\qquad\qquad\times G(a-b,t-b,P_{lm}(t-b))\Big|\,db\,da
\end{aligned}
$$

$$
\begin{aligned}
\le \int_0^t\int_0^a &\left|\exp\left(-\int_{t-b}^{t}\Delta_{m}(s+a-t,s+b-t,s,P_{lm}(s))\,ds\right)\right.\\
&\times G(a-b,t-b,P_{lm}(t-b))\\
&-\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\\
&\times G(a-b,t-b,P_{lm}(t-b))\\
&+\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\\
&\times G(a-b,t-b,P_{lm}(t-b))\\
&-\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\\
&\qquad\qquad\left.\times G(a-b,t-b,P_{l'm'}(t-b))\right|\,db\,da
\end{aligned}
$$

$$
\begin{aligned}
\le \int_0^t\int_0^a\int_{t-b}^{t} &\big|\Delta_{m}(s+a-t,s+b-t,s,P_{lm}(s))\\
&\qquad-\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\big|\,ds\\
&\times\left|G(a-b,t-b,P_{lm}(t-b))\right|\,db\,da\\
&+\int_0^t\int_0^a\left|\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t,s+b-t,s,P_{l'm'}(s))\,ds\right)\right|\\
&\times\big|G(a-b,t-b,P_{lm}(t-b))\\
&\quad G(a-b,t-b,P_{l'm'}(t-b))\big|\,db\,da.
\end{aligned}
$$

Consider these last two integrals,

$$\int_0^t \int_0^a \int_{t-b}^t \big| \Delta_m(s+a-t, s+b-t, s, P_{lm}(s)) - \Delta_{m'}(s+a-t, s+b-t, s, P_{l'm'}(s)) \big| \, ds \times \big| G(a-b, t-b, P_{lm}(t-b)) \big| \, db \, da, \tag{2.18}$$

and

$$\int_0^t \int_0^a \left| \exp\left(-\int_{t-b}^t \Delta_{m'}(s+a-t, s+b-t, s, P_{l'm'}(s)) \, ds \right) \right| \times \big| G(a-b, t-b, P_{lm}(t-b)) - G(a-b, t-b, P_{l'm'}(t-b)) \big| \, db \, da. \tag{2.19}$$

To see how the estimate for (2.18) is done, see the computation for integral (2) in the following text. Expression (2.19) is estimated as follows,

$$\begin{aligned}
&\int_0^t \int_0^a \left| \exp\left(-\int_{t-b}^t \Delta_{m'}(s+a-t, s+b-t, s, P_{l'm'}(s)) \, ds \right) \right| \\
&\quad \times \big| G(a-b, t-b, P_{lm}(t-b)) - G(a-b, t-b, P_{l'm'}(t-b)) \big| \, db \, da \\
&\quad \le \int_0^t \int_0^a \big| G(a-b, t-b, P_{lm}(t-b)) - G(a-b, t-b, P_{l'm'}(t-b)) \big| \, db \, da \\
&\quad \le \int_0^t \int_0^a \bigg| \pi_l(a-b, t-b, P_{l,m}(t-b)) L(a-b, t-b) \\
&\qquad + \int_0^{a-b} \pi_m(a-b, s_1, t-b, P_{lm}(t-b)) \times M(a-b, s_1, t-b) \, ds_1 \\
&\qquad - \pi_{l'}(a-b, t-b, P_{l'm'}(t-b)) L'(a-b, t-b) \\
&\qquad - \int_0^{a-b} \pi_{m'}(a-b, s_1, t-b, P_{l'm'}(t-b)) \times M'(a-b, s_1, t-b) \, ds_1 \bigg| \, db \, da \\
&\quad \le \int_0^t \int_0^a \big| \pi_l(a-b, t-b, P_{l,m}(t-b)) L(a-b, t-b) - \pi_{l'}(a-b, t-b, P_{l'm'}(t-b)) L'(a-b, t-b) \big| \, db \, da
\end{aligned}$$

$$+\int_0^t\int_0^a\int_0^{a-b}\left|\pi_m(a-b,s_1,t-b,P_{lm}(t-b))M(a-b,s_1,t-b)\right.$$
$$-\pi_{m'}(a-b,s_1,t-b,P_{l'm'}(t-b))$$
$$\left.\times M'(a-b,s_1,t-b)\right|ds_1.$$

These last two integrals are estimated similarly. Consider the first: we will employ the *a priori* estimate on (L,M) in the previous text—recall that $t\le T<\infty$),

$$\int_0^t\int_0^a\left|\pi_l(a-b,t-b,P_{l,m}(t-b))L(a-b,t-b)\right.$$
$$\left.-\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L'(a-b,t-b)\right|db\,da$$
$$\le\int_0^t\int_0^a\left|\pi_l(a-b,t-b,P_{l,m}(t-b))L(a-b,t-b)\right.$$
$$-\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L(a-b,t-b)$$
$$+\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L(a-b,t-b)$$
$$\left.-\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L'(a-b,t-b)\right|db\,da$$
$$\le\int_0^t\int_0^a\left|\pi_l(a-b,t-b,P_{l,m}(t-b))L(a-b,t-b)\right.$$
$$\left.-\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L(a-b,t-b)\right|db\,da$$
$$+\int_0^t\int_0^a\left|\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L(a-b,t-b)\right.$$
$$\left.-\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))L'(a-b,t-b)\right|db\,da$$
$$\le\int_0^t\int_0^a\left|P_{l,m}(t-b)-P_{l'm'}(t-b)\right|\left|L(a-b,t-b)\right|db\,da$$
$$+\int_0^t\int_0^a\left|\pi_{l'}(a-b,t-b,P_{l'm'}(t-b))\right|\left|L(a-b,t-b)\right.$$
$$\left.-L'(a-b,t-b)\right|db\,da$$
$$\le\int_0^t\int_0^a\left|(I,M)(t-b)-(I',M')(t-b)\right|_{L^1}\left|L(a-b,t-b)\right|db\,da$$
$$+\int_0^t\int_0^a\left|\pi_{l'}(\cdot,t-b,P_{l'm'}(t-b))\right|_\infty\left|L(a-b,t-b)\right.$$
$$\left.-L'(a-b,t-b)\right|e^{-r(t-b)}e^{r(t-b)}\,db\,da$$

$$\leq \int_0^t |(L,M)(t-b)-(L',M')(t-b)|_{L^1} e^{-r(t-b)} e^{r(t-b)}$$

$$\times \int_b^t |L(a-b,t-b)|\, da\, db$$

$$+\int_0^t \int_b^t |\pi_{l'}(\cdot, t-b, P_{l'm'}(t-b))|_\infty$$

$$\times |L(a-b,t-b)-L'(a-b,t-b)| e^{-r(t-b)} e^{r(t-b)}\, da\, db$$

$$\leq J|(L,M)-(L',M')|_{X_r} \int_0^t e^{r(t-b)}\, db$$

$$\leq J_1 |(L,M)-(L',M')|_{X_r} \frac{e^{rt}}{r}, \tag{2.20}$$

for some constant J_1. The other integrals deriving from (4) are estimated similarly.

Consider the integral (2). We have

$$(2) + \int_0^t \Big| \exp\Big(-\int_{t-a}^t \Delta_l(s-t+a, s, P_{lm}(s))\, ds \Big) C(t-a, P_{lm}(t-a))$$

$$- \exp\Big(-\int_{t-a}^t \Delta_{l'}(s-t+a, s, P_{l'm'}(s))\, ds \Big) C(t-a, P_{l'm'}(t-a)) \Big|\, da$$

$$\leq \int_0^t \Big| \exp\Big(\int_{t-a}^t -\Delta_l(s-t+a, s, P_{lm}(s))\, ds \Big) C(t-a, P_{lm}(t-a))$$

$$- \exp\Big(\int_{t-a}^t -\Delta_{l'}(s-t+a, s, P_{l'm'}(s))\, ds \Big)$$

$$\times C(t-a, P_{lm}(t-a))$$

$$+ \exp\Big(\int_{t-a}^t -\Delta_{l'}(s-t+a, s, P_{l'm'}(s))\, ds \Big)$$

$$\times C(t-a, P_{lm}(t-a))$$

$$- \exp\Big(\int_{t-a}^t -\Delta_{l'}(s-t+a, s, P_{l'm'}(s))\, ds \Big)$$

$$\times C(t-a, P_{l'm'}(t-a)) \Big|\, da$$

$$\leq \int_0^t \int_{t-a}^t \left|\Delta_l(s-t+a, s, P_{lm}(s)) - \Delta_{l'}(s-t+a, s, P_{l'm'}(s))\right| ds$$

$$\times \left|C(t-a, P_{lm}(t-a))\right| da$$

$$+ \int_0^t \exp\left(\int_{t-a}^t - \Delta_{l'}(s-t+a, s, P_{l'm'}(s))\, ds\right)$$

$$\times \left|C(t-a, P_{lm}(t-a)) - C(t-a, P_{l'm'}(t-a))\right| da$$

$$\leq \int_0^t \int_{t-a}^t \left|P_{lm}(s) - P_{l'm'}(s)\right| ds \left|C(t-a, P_{lm}(t-a))\right| da$$

$$+ \int_0^t \left|C(t-a, P_{lm}(t-a)) - C(t-a, P_{l'm'}(t-a))\right| da$$

$$\leq \int_0^t \int_{t-a}^t \left|I(L, M)(s) - I(L', M')(s)\right| e^{-rs} e^{rs}\, ds\, K \left|P_{lm}(t-a)\right| da$$

$$+ \int_0^t \left|C(t-a, P_{lm}(t-a)) - C(t-a, P_{l'm'}(t-a))\right| da.$$

Recall that

$$C(t-a, P_{lm}(t-a))$$

$$= \int_0^U B(s, t-a, P_{lm}(t-a)) L(s, t-a)\, ds$$

$$+ \int_0^U \int_0^s \Gamma(s, b, t-a, P_{lm}(t)) M(s, b, t-a)\, db\, ds.$$

Therefore,

$$\int_0^t \left|C(t-a, P_{lm}(t-a)) - C(t-a, P_{l'm'}(t-a))\right| da$$

$$\leq \int_0^t \int_0^U \left| B(s, t-a, P_{lm}(t-a)) L(s, t-a) \right.$$

$$\left. - B(s, t-a, P_{l'm'}(t-a)) L'(s, t-a) \right| ds\, da$$

$$+ \int_0^t \int_0^U \int_0^s \left| \Gamma(s, b, t-a, P_{lm}(t)) M(s, b, t-a) \right.$$

$$\left. - \Gamma(s, b, t-a, P_{l'm'}(t)) M'(s, b, t-a) \right| db\, ds\, da.$$

Now a computation similar to that found in (2.20), gives a similar estimate.

Hence we obtain the estimates,

$$\left|I(L, M) - I(L', M')\right|_{L^1}(t) \leq \frac{e^{rt}}{r} J \left|(L, M) - (L', M')\right|_{X_r},$$

for some constant J. Thus,

$$|I(L,M) - I(L',M')|_{X_r} \leq \frac{1}{r} J |(L,M) - (L',M')|_{X_r}. \quad (2.21)$$

If $r > J$, then I is a strict contradiction on a closed subspace of the Banach space X_r and so has a fixed point there. Consequently, there exists a unique solution to the system in X. This completes the proof of Theorem 2.

COROLLARY 1. *The components of* (L, M) *are nonnegative if* (L_o, M_o) *has nonnegative components.*

Proof. The result follows when we note that by the contraction mapping theorem, a solution to the migration problem may be obtained by iteration of I on some initial value. If the initial point is chosen so that it has nonnegative components, then the iterates clearly have nonnegative components and so the limit also has this property.

We now derive some useful estimates on the solution of the migration problem. We know that any solution ${}^t(L(a,t), M(a,b,t))$ has population vector $P(t)$, norm bounded by $ce^{\kappa t}$ for some c and κ, and c can be taken as $|P(0)|$ (see (2.17)).

Define $\Delta_1 = \min|\Delta_l(a,t)|$, $\Delta_2 = \min|\Delta_m(a,b,t)|$). From (2.8)–(2.11), $(a > t > b)$,

$$\begin{aligned} G(a,t,P_{lm}) = \pi_l(a,t,P_{lm}(t))L(a,t) + \int_0^a &\pi_m(a,b,t,P_{lm}(t)) \\ &\times \exp\left(-\int_{t-b}^t \Delta_m(s+a-t, s+b-t, s, P_{lm}(s))\, ds\right) \\ &\times G(a-b, t-b, P_{lm}(t-b))\, db. \end{aligned} \quad (2.22)$$

So we can rewrite the equation for G,

$$\begin{aligned} G(a,t) = {}&\pi_l(a,t,P_{l,m})L(a,t) \\ &+ \int_0^a K(a,b,t,P_{lm}) G(a-b, t-b)\, db, \end{aligned} \quad (2.23)$$

with the change of variables,

$$\tilde{G}(r,s) = G(s, r+s), \quad (2.24)$$

we have

$$\begin{aligned} \tilde{G}(\alpha, a) = {}&\pi_l(a, \alpha + a, P_{l,m}) L(a, \alpha + a) \\ &+ \int_0^a K(a,b,\alpha + a, P_{lm}) \tilde{G}(\alpha, a-b)\, db. \end{aligned} \quad (2.25)$$

This is a Volterra equation and hence has a unique solution in L^1. K contains the exponential part,

$$\exp\left(-\int_{t-b}^{t}\Delta_m(s+a-t, s+b-t, s, P_{lm}(s))\,ds\right), \tag{2.26}$$

and we assume π_l, π_m are bounded by constants, C_1 and C_2, respectively. Then from

$$\begin{aligned}(5)\int_t^U\int_0^t \Bigg| &\exp\left(-\int_{t-b}^{t}\Delta_m(s+a-t, s+b-t, s, P_{lm}(s))\,ds\right)\\ &\times G(a-b, t-b, P_{lm}(t-b))\\ &-\exp\left(-\int_{t-b}^{t}\Delta_{m'}(s+a-t, s+b-t, s, P_{l'm'}(s))\,ds\right)\\ &\times G(a-b, t-b, P_{l'm'}(t-b))\Bigg|\,db\,da,\end{aligned} \tag{2.27}$$

we have,

$$\left|\tilde{G}(\alpha, a)\right| \le C_1 e^{-\Delta_1 a} + C_2\int_0^a e^{-\Delta_2(a-s)}\left|\tilde{G}(\alpha, s)\right|ds. \tag{2.28}$$

So,

$$e^{\min(\Delta_1,\Delta_2)a}\left|\tilde{G}(\alpha, a)\right| \le C_1 + C_2\int_0^a e^{\min(\Delta_1,\Delta_2)s}\left|\tilde{G}(\alpha, s)\right|ds. \tag{2.29}$$

Gronwall's inequality implies that

$$\left|\tilde{G}(\alpha, a)\right| \le C_1 e^{(C_2-\min(\Delta_1,\Delta_2))a}, \tag{2.30}$$

or

$$\left|G(a, t)\right| \le C_1 e^{(C_2-\min(\Delta_1,\Delta_2))a}, \tag{2.31}$$

this implies

$$\left|G(a-b, t-b, P_{lm}(t-b))\right| \le C_1 e^{(C_2-\min(\Delta_1,\Delta_2))(a-b)}, \tag{2.32}$$

$$\begin{aligned}C(t, P_{lm}) = L(0,t) = \int_0^U & B(a, t, P_{lm}(t))L(a,t)\,da\\ &+\int_0^U\int_0^a \Gamma(a, b, t, P_{lm}(t))M(a, b, t)\,db\,da.\end{aligned} \tag{2.33}$$

Therefore,

$$\begin{aligned} \left|C(t, P_{lm})\right| \leq & \int_0^U \left|B\big(a, t, P_{lm}(t)\big)\right| \left|L(a, t)\right| da \\ & + \int_0^U \int_0^a \left|\Gamma\big(a, b, t, P_{lm}(t)\big)\right| \left|M(a, b, t)\right| db\, da. \end{aligned} \tag{2.34}$$

We assumed that B and G were bounded by D_1 and D_2, respectively. Then

$$\left|C(t, P_{lm})\right| \leq D_1 \int_0^U \left|L(a, t)\right| da + D_2 \int_0^U \int_0^a \left|M(a, b, t)\right| db\, da. \tag{2.35}$$

Hence,

$$\left|C(t, P_{lm})\right| \leq \max(D_1, D_2) P(t) \leq \max(D_1, D_2) c e^{\kappa t}, \tag{2.36}$$

and so

$$\begin{aligned} \left|C\big(t - a, P_{lm}(t - a)\big)\right| & \leq \max(D_1, D_2) P_{lm}(t - a) \\ & \leq \max(D_1, D_2) c e^{\kappa(t-a)}. \end{aligned} \tag{2.37}$$

Using (2.10) and (2.11) we can now write

$$\begin{aligned} & \left|\big(L(a, t), M(a, b, t)\big)\right| \\ & \quad \leq e^{-\Delta_1 t} \max\left|L_o(a - t)\right| + e^{-\Delta_2 t} \max\left|M_o(a - t, b - t)\right|, \\ & \qquad (t < b), \end{aligned} \tag{2.38}$$

$$\begin{aligned} & \left|\big(L(a, t), M(a, b, t)\big)\right| \\ & \quad \leq e^{-\Delta_1 t} \max\left|L_o(a - t)\right| \\ & \qquad + e^{-\Delta_2 b}\Big(K_1 \max\left|L_o(a - t)\right| + C_1 e^{(C_2 - \min(\Delta_1, \Delta_2)a)}\Big), \\ & \qquad (a > t > b), \end{aligned} \tag{2.39}$$

$$\begin{aligned} & \left|\big(L(a, t), M(a, b, t)\big)\right| \\ & \quad \leq e^{-\Delta_1 a} \max(D_1, D_2) c e^{\kappa t} \\ & \qquad + e^{-\Delta_2 b}\Big(\max(D_1, D_2) c e^{\kappa(t-a)} + C_1 e^{(C_2 - \min(\Delta_1, \Delta_2)a)}\Big), \\ & \qquad (t > a > b). \end{aligned} \tag{2.40}$$

We can therefore state the following

THEOREM 3. *If* (L, M) *is a solution to the migration problem, then the estimates* (2.37)–(2.40) *hold*.

3. EQUILIBRIUM SOLUTIONS

When the coefficients Δ, β, γ, and the π functions do not depend on time, it is of interest to determine if equilibrium solutions (zero velocity populations) are possible.

The time-independent equations are

$$Dl_i(a,t) = -\mu_{l_i}(a,P)l_i(a,t) - \sum_j \pi_{ji}(a,P)l_i(a,t)$$

$$\left(\sum_j \text{ indicates summation on } j\right), \quad (3.1)$$

$$Dm_i(a,b,t) = -\mu_{m_i}(a,b,P)m_i(a,b,t) - \sum_j \pi_{ji}(a,b,P)m_i(a,b,t). \quad (3.2)$$

For an equilibrium solution (L_e, M_e) and the associated population vector P_e, we arrive at the following equations,

$$\frac{\partial L_e}{\partial a} = -\Delta_l(a,P_e)L(a), \quad (3.3)$$

$$L_e(0) = \int_0^U B(a,P_e)L_e(a)\,da + \int_0^U\int_0^a \Gamma(a,b,P_e)M_e(a,b)\,db\,da, \quad (3.4a)$$

$$M_e(a,0) = \pi_l(a,P_e)L_e(a) + \int_0^a \pi_m(a,b,P_e)M_e(a,b)\,db, \quad (3.4b)$$

$$\frac{\partial M_e}{\partial a} + \frac{\partial M_e}{\partial b} = -\Delta_m(a,b,P_e)M_e(a,b). \quad (3.5)$$

Equation (3.3) may be solved as

$$L_e(a) = \exp\left(\int_0^a -\Delta_l(s,P_e)\,ds\right)L_e(0), \quad (3.6)$$

Eq. (3.5) may be solved as

$$M_e(a,b) = \exp\left(\int_0^b -\Delta_m(a-b+s,s,P_e)\,ds\right)M_e(a-b,0), \quad (3.7)$$

Eqs. (3.6) and (3.7) allow us to write (3.4a, b) as a system for $L_e(0)$, $M_e(a,0)$,

$$L_e(0) = \int_0^U B(a, P_e)\exp\left(\int_0^a -\Delta_l(s, P_e)\,ds\right) da\, L_e(0)$$
$$+\int_0^U\int_0^a \Gamma(a, b, P_e)\exp\left(\int_0^b -\Delta_m(a-b+s, s, P_e)\,ds\right)$$
$$\times M_e(a-b, 0)\,db\,da \tag{3.8a}$$

$$M_e(a,0) = \pi_l(a, P_e)\exp\left(\int_0^a -\Delta_l(s, P_e)\,ds\right) L_e(0)$$
$$+\int_0^a \pi_m(a, b, P_e)\exp\left(\int_0^b -\Delta_m(a-b+s, s, P_e)\,ds\right)$$
$$\times M_e(a-b, 0)\,db. \tag{3.8b}$$

If

$$Q = \left(I - \int_0^U B(a, P_e)\exp\left(\int_0^a -\Delta_l(s, P_e)\,ds\right) da\right)$$

is invertible, then the first equation may be solved for $L_e(0)$. Substituting into the second equation, we have an expression containing only $M_e(s, 0)$. Define τ by the equation,

$$\tau = \int_0^U\int_0^a \Gamma(a, b, P_e)\exp\left(\int_0^b -\Delta_m(a-b+s, s, P_e)\,ds\right)$$
$$\times M_e(a-b, 0)\,db\,da, \tag{3.9}$$

then $L_e(0) = Q^{-1}\tau$, where $\tau = \tau(M_e, P_e)$, $Q = Q(P_e)$, τ is linear in M_e. Then we have

$$M_e(a,0) = \pi_l(a, P_e)\exp\left(\int_0^a -\Delta_l(s, P_e)\,ds\right) Q^{-1}(P_e)\tau(M_e, P_e)$$
$$+\int_0^a \pi_m(a, b, P_e)\exp\left(\int_0^b -\Delta_m(a-b+s, s, P_e)\,ds\right)$$
$$\times M_e(a-b, 0)\,db. \tag{3.10}$$

If we consider the equation,

$$Z(a) = \pi_l(a, P_e)\exp\left(\int_0^a -\Delta_l(s, P_e)\,ds\right) Q^{-1}(P_e)$$
$$+\int_0^a \pi_m(a, b, P_e)\exp\left(\int_0^b -\Delta_m(a-b+s, s, P_e)\,ds\right)$$
$$\times Z(a-b)\,db, \tag{3.11}$$

we see that it is a Volterra equation. Multiplying the solution $Z(a)$ on the right by $\tau(M_e, P_e)$, we obtain $M_e(a,0) = Z(a)\tau(M_e, P_e)$. If a solution exists, then the system has an equilibrium solution ($M_e(a,0) = 0$ is certainly such a solution, but then (3.8a) implies that $L_e(0) = 0$).

If however $Q = 0$, then we conclude from (3.8a) that $M_e(a,0) = 0$. In that case, (3.8b) is satisfied when $L_e(0)$ is always in the kernel of

$$\pi_l(a, P_e)\exp\left(\int_0^a -\Delta_l(s, P_e)\,ds\right). \tag{3.12}$$

Therefore an equilibrium solution exists if there is such a value P_e (and essentially this says that $L_e(0)$ does not evolve to migrate to other patches). Hence, an equilibrium solution exists when Q^{-1} exists (though possibly only the trivial solution), and if $Q = 0$ for some P_e, a nontrivial equilibrium solution may exist. When $Q = 0$, the solution may possibly be chosen so that $L_e(0) \neq 0$, but $M_e(a,0) = 0$. It may happen that some of the entries of Q do not vanish, while some do for any given P_e. Then we could have a solution of mixed character, but essentially the same analysis applies in this case, coordinate by coordinate in (3.8a) because Γ and B are diagonal matrices. To investigate further, define

$$\begin{aligned} P_{el} &= \int_0^U L_e(a)\,da, \\ P_{em} &= \int_0^U \int_0^a M_e(a,b)\,db\,da, \end{aligned} \tag{3.13}$$

$$P_e = P_{el} + P_{em}. \tag{3.14}$$

Integrating both sides of (3.6) gives

$$L_e(0) = \left(\int_0^U \exp\left(-\int_0^a -\Delta_l(s, P_e)\,ds\right)da\right)^{-1} P_{el}, \tag{3.15}$$

consequently,

$$QL_e(0) = Q\left(\int_0^U \exp\left(-\int_0^a -\Delta_l(s, P_e)\,ds\right)da\right)^{-1}, \qquad P_{el} = \tau(M_e, P_e), \tag{3.16}$$

and so if Q^{-1} exists,

$$M_e(a,0) = Z(a)Q(P_e)\left(\int_0^U \exp\left(-\int_0^a -\Delta_l(s, P_e)\,ds\right)da\right)^{-1} P_{el}. \tag{3.17}$$

Therefore, if Q^{-1} exists, we have

$$
\begin{aligned}
L_e(a) &= \exp\left(\int_0^a - \Delta_l(s, P_e)\, ds\right) L_e(0), \\
M_e(a, b) &= \exp\left(\int_0^b - \Delta_m(a - b + s, s, P_e)\, ds\right) M_e(a - b, 0), \\
L_e(0) &= \left(\int_0^U \exp\left(-\int_0^a - \Delta_l(s, P_e)\, ds\right) da\right)^{-1} P_{el}, \\
M_e(a, 0) &= Z(a) Q(P_e) \left(\int_0^U \exp\left(-\int_0^a G - \Delta_l(s, P_e)\, ds\right) da\right)^{-1} P_{el}.
\end{aligned}
\tag{3.18}
$$

Because the matrices in (3.8a) are all diagonal, this (the existence of Q^{-1}) provides a simple test to determine the existence of equilibrium solutions.

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