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MIGRATION IN AGE STRUCTURED POPULATION DYNAMICS

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We introduce a linear model for age structured populations which migrate between several locations or patches. Birth is allowed in each patch. Existence, uniqueness and positivity of solutions is proved. A certain North Atlantic fishery is given as an example. Asymptotic solutions are characterized in a general system with periodic coefficients by spectral theory techniques and the results are applied to the example.

1. Introduction

Structured population models of continuous type have received varying degrees of attention in the last two decades. Ecologists, mathematicians and population biologists have observed that structure variables provide more realistic results at reasonable computational expense for a wide variety of bio-populations.[1,4,6,9] Considerably less work has been done in incorporating migration effects in structured models outside of diffusion. See references in Webb[10] for example.

Our purpose here is to introduce a model with age-structure (although size or other structure variables are easily added) which contains a simple account of the sort of migration effects widely observed in bio-populations such as fish and bird populations.

The model is a partial differential equation model with boundary conditions of the renewal equation type. In Sec. 1 we prove that a unique solution exists for the model with appropriate initial conditions. In Sec. 2 we illustrate how this model may be applied to a certain fishery problem by considering the species *pollachius virens*. This fish is better known as the *saithe*. The life history of the saithe may be added to the model, such as periodic birth and transfer (migration) coefficients. When these conditions are added, the solutions for large time have a special character which can be investigated in the general setting of the model. In Sec. 3, we add these extra conditions regarding periodic coefficients and then study the asymptotic behavior of solutions (for large time).

We consider a population of $N(\geq 2)$ numbers divided among patches or locations. Patches may be thought of as distinct but spatial overlap is not excluded in general. Population segments are further distinguished in terms of migratory status:

> $\ell_i(a,t)$ is the density of individuals who were born at time t in patch i and have remained up to age a. $m_i(a,b,t)$ is the density of those individuals at time t in patch i which have attained age a and are migrants from other patches, having lived in patch i for time b, $(b < a)$.

Individuals are assumed to have a maximum possible age U. The total population in patch i is given by

$$P_i(t) = \int_0^U \ell_i(a,t)\,da + \int_0^U \int_0^a m_i(a,b,t)\,db\,da\,. \tag{1.1}$$

Birth and migration rates may be characterized in terms of boundary conditions on ℓ_i, m_i, $1 \leq i \leq N$ as

$$\ell_i(0,t) = \int_0^U \beta_i(a,t)\ell_i(a,t)\,da + \int_0^U \int_0^a \gamma_i(a,b,t)m_i(a,b,t)\,db\,da\,, \tag{1.2}$$

where $\beta_i(a,t)$ is the fertility rate for natives of patch i, while $\gamma_i(a,b,t)$ represents the fertility of migrants, possibly different from that of natives in patch i. γ_i is a simplification since m_i represents individuals from many other locations who may each have different adaptive fecundity.

To model migration rate, we employ the proportionality migration rates (from patch j to patch i) $\pi_{\ell ij}(a,t)$, $\pi_{mij}(a,b,t)$, which are non-negative functions such that

$$m_i(a,0,t) = \sum_{j\neq i} \pi_{\ell ij}(a,t)\ell_j(a,t) + \sum_{j\neq i} \int_0^a \pi_{mij}(a,b,t)m_j(a,b,t)\,db\,. \tag{1.3}$$

Finally we require population death rates which may be different for migrants and natives in a given patch.

Death rate for natives in patch i is given by $\mu_{\ell i}(a,t) \geq 0$.

Death rate for migrants in patch i is given by $\mu_{mi}(a,b,t) \geq 0$.

Death rates are allowed to be age, time and time-in-patch dependent. Since all individuals die by age U, we assume that $\mu_{\ell_i}(a,t)$, $\mu_{mi}(a,b,t)$ (for each t,b) approach infinity as $a \to U$, but are bounded for $a < r < U$, uniformly in t,b, where r is any fixed age.

The equations describing the rate of change for $m_i, \ell_i, 1 \le i \le N$, are

$$\frac{\partial \ell_i}{\partial t} + \frac{\partial \ell_i}{\partial a} = -\mu \ell_i(a,t)\ell_i(a,t) - \sum_{j \neq i} \pi \ell_{ji}(a,t)\ell_i(a,t)\,, \tag{1.4}$$

$$\frac{\partial m_i}{\partial t} + \frac{\partial m_i}{\partial a} + \frac{\partial m_i}{\partial b} = -\mu_{mi}(a,b,t)m_i(a,b,t) - \sum_{j \neq 1} \pi_{mji}(a,b,t)m_i(a,b,t)\,, \tag{1.5}$$

$$\ell_i(a,0) = \ell_{i0}(a)\,, \quad 0 \le a \le U \tag{1.4a}$$

$$m_i(a,b,0) = m_{i0}(a,b)\,, \quad 0 \le b < a < U\,. \tag{1.5a}$$

To simplify our study of these equations, we introduce some notation. (${}^tA$ means transpose of A).

$$\Omega = \{(a,b) : 0 \le b < a < U\}\,,$$

$$M(a,b,t) = {}^t(m_1(a,b,t), m_2(a,b,t), \ldots, m_N(a,b,t)) \in \mathbb{R}^N\,,$$

$$M_0(a,b) = M(a,b,0)\,,$$

$$L(a,t) = {}^t(\ell_1(a,t), \ell_2(a,t), \ldots, \ell_N(a,t)) \in \mathbb{R}^N\,,$$

$$L_0(a) = L(a,0)\,,$$

$$\pi_\ell(a,t) = [\pi_{\ell ji}(a,t)]\,, \text{ where } 1 \le i \le N,\ 1 \le j \le N$$

$$\pi_m(a,b,t) = [\pi_{mji}(a,b,t)]\,, \text{ where } 1 \le i \le N,\ 1 \le j \le N$$

$$\Delta_{\ell_i}(a,t) = \mu_{\ell i}(a,t) + \sum_{i \neq j} \pi_{ji}(a,t)\,,$$

$$\Delta_\ell(a,t) = \text{diag}(\Delta_{\ell_i}(a,t)) \text{ (the diagonal matrix with entries } \Delta_{\ell_i} \text{ on the main diagonal)}$$

$$\Delta_{m_i}(a,b,t) = \mu_{mi}(a,b,t) + \sum_{i \neq j} \pi_{ji}(a,b,t)\,,$$

$$\Delta_m(a,b,t) = \text{ diag } (\Delta_{m_i}(a,b,t))\,,$$

$$B(a,t) = \text{ diag}(\beta_i(a,t)),$$

$$\Gamma(a,b,t) = \text{diag}(\gamma_i(a,b,t))\,.$$

The matrices $\Delta_\ell, \Delta_m, \pi_\ell, \pi_m, B$ and Γ have all non-negative entries. Vectors and matrix norms are denoted by $|\cdot|$.

The observation that

$$\frac{dL}{dh}(h,h+q) = \frac{\partial L}{\partial t}(h,h+q) + \frac{\partial L}{\partial a}(h,h+q) \tag{1.6}$$

and

$$\frac{dM}{dh}(q+h,h,r+h) = \frac{\partial M}{\partial a} + \frac{\partial M}{\partial b} + \frac{\partial M}{\partial t}\,, \tag{1.7}$$

allows us to write Eqs. (1.4)–(1.5) as

$$L(a,t) = \begin{cases} \exp\left(-\int_0^t \Delta_\ell(s+a-t,s)\,ds)\,ds\right) L_0(a-t)\,, & t<a\,, \\ \exp\left(-\int_{t-a}^t \Delta_\ell(s+a-t,s)\,ds\right) L(0,t-a)\,, & t>a\,, \end{cases} \tag{1.8}$$

$$M(a,b,t) = \begin{cases} \exp\left(-\int_0^t \Delta_m(s+a-t,s+b-t,s)\,ds\right) M_0(a-t,b-t)\,, & t<b\,, \\ \exp\left(-\int_0^b \Delta_m(a-b+s,s,s+t-b)\,ds\right) M(a-b,0,t-b)\,, & t>b\,. \end{cases} \tag{1.9}$$

Note that the matrix exponentials in (1.8), (1.9) have norm bounded by 1. Using the substitutions of (1.6), (1.7) shows the formal equivalence of (1.8), (1.9) to (1.4), (1.5). At this point we can make the necessary precise assumptions to construct a setting in which existence of M and L may be proved.

2. Existence, Uniqueness and Positivity

In the sequel, we do not use the boundary values of L and M as pointwise quantities; our formulation is a weak one. We assume that the functions B, Γ, π_ℓ and π_m are measurable and for any $T>0$, they are essentially bounded for $t \le T$. The functions Δ_ℓ, Δ_m are assumed measurable with $|\Delta_\ell(a,t)| \to \infty$ as $a \to U$ for almost all $t \le T$. Likewise, $|\Delta_m(a,b,t)| \to \infty$ as $a \to U$ for almost all $b<a$, $t<T$. If $r<U$, then $|\Delta_\ell|, |\Delta_m|$ are essentially bounded for $a \in [0,r]$. Finally, the entries of $\pi_\ell, \pi_m, \Delta_\ell, \Delta_m, B$ and Γ are assumed to be non-negative almost everywhere.

Definition 2.1.[3] Let X_r be the set of essentially bounded functions on $[0,T]$ with range in $L^1(0,U,\mathbb{R}^N) \times L^1(\Omega,\mathbb{R}^N)$.

$F \in X_r$ means F has the form

$$F = {}^t(\ell_1(a,t),\ell_2(a,t),\ldots,\ell_N(a,t),m_1(a,b,t),m_2(a,b,t),\ldots,m_N(a,b,t))\,, \tag{2.1}$$

$$F(t) = \begin{pmatrix} L \\ M \end{pmatrix}. \tag{2.2}$$

The norm in X_r is defined by

$$\|F\|_{X_r} = \left\| \begin{pmatrix} L \\ M \end{pmatrix} \right\|_{X_r} = \operatorname*{ess\,sup}_{t\in[0,T]} e^{-rt}\left[|L(\cdot,t)|_1 + |M(\cdot,\cdot,t)|_1\right]. \tag{2.3}$$

We define $X = X_0$.

The notation $|L(\cdot,t)|_1$, means $\int_0^u |L(a,t)|\,da$, $|M(\cdot,\cdot,t)|_1$, means

$$\int_0^U \int_0^a |M(a,b,t)|\,db\,da\,.$$

The norms $|I^t(L,M)(a,t)\times(a,b,t)|$, $|I^t(L,M)(\cdot,t)\times(\cdot,\cdot,t)|_1$ are used. The notation ${}^t(L,M)$ means the transpose of the $2N$-vector (L,M). Hence $|I^t(L,M)(a,t)\times(a,b,t)|$ merely means the Euclidean $2N$-norm of the vector function $I^t(L,M)$, as defined by the conjoining of the N vectors defined by the right-hand sides of (1.8) and (1.9), respectively. The notation $|I^t(L,M)(\cdot,t)\times(\cdot,\cdot,t)|_1$ means the sum of the norms (defined above) of the N-vector valued functions given by the right-hand sides of (1.8) and (1.9), respectively.

The expressions $L(0,t), L(a,0)$, etc. are not well-defined in X_r, but the right-hand sides of (1.2), (1.3), (1.4a) and (1.5a) are defined in X_r. We will therefore use the right-hand sides of (1.2), (1.3), (1.4a), (1.5a) in (1.8), (1.9) in order to prove an existence theorem in X. In the classical case, solutions of (1.8), (1.9) coincide with those of (1.2)–(1.5a).

Define $I : X_r \to X_r$ by the right-hand side of (1.8) and (1.9) together. To show that a solution exists for Eqs. (1.8) and (1.9), we will show that I has a fixed point in X_r, for sufficiently large r.

The boundary conditions (1.2), (1.3) may be restated in vector form as

$$u(t) = L(0,t) = \int_0^U B(a,t)L(a,t)\,da + \int_0^U \int_0^a \Gamma(a,b,t)M(a,b,t)\,db\,da\,, \tag{2.4}$$

$$v(a,t) = M(a,0,t) = \pi_\ell(a,t)L(a,t) + \int_0^a \pi_m(a,s,t)M(a,s,t)\,ds\,. \tag{2.5}$$

By (1.8), (1.9) we have

$$|I^t(L,M)(a,t)\times(a,b,t)| \le \begin{cases} |L_0(a-t)| + |M_0(a-t,b-t)|\,, & t<b<a\,,\\ |L_0(a-t)| + |v(a-b,t-b)|\,, & b<t<a\,,\\ |u(t-a)| + |v(a-b,t-b)|\,, & b<a<t\,. \end{cases} \tag{2.6}$$

To show that I is well-defined on X_r, we integrate both sides of (2.6) to get

$$\begin{aligned} &|I^t(L,M)(\cdot,t)\times(\cdot,\cdot,t)|_1 \\ &\quad \le \int_t^a |L_0(s-t)|\,ds + \int_0^U \int_t^a |M_0(a-t,b-t)\,db\,da \\ &\qquad + \int_t^T \int_0^t |\pi_\ell(a-b,t-b)||L(a-b,t-b)|\,db\,da \end{aligned}$$

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

$$+\int_0^t |u(t-a)|\,da + \int_0^t \int_0^a |\pi_\ell(a-b,t-b)||L(a-b,t-b)|\,db\,da$$

$$+\int_0^t \int_0^a \int_0^{a-b} |\pi_m(a-b,s,t-b)||M(a-b,s,t-b)|\,ds\,db\,da\,. \qquad (2.7)$$

We observe that

$$\begin{aligned}\int_0^t |u(t-a)|\,da &\le \int_0^t \int_0^U |B(s,t-a)||L(s,t-a)|\,ds\,da \\ &\qquad + \int_0^t \int_0^U \int_0^a |\Gamma(s,s_1,t-a)||M(s,s_1,t-a)|\,ds\,ds_1\,da \\ &\le \int_0^t |B(\cdot,t-a)|_\infty |L(\cdot,t-a)|_1\,da \\ &\qquad + \int_0^t |\Gamma(\cdot,\cdot,t-a)|_\infty |M(\cdot,\cdot,t-a)|_1\,da\,. \end{aligned} \qquad (2.8)$$

Also note that when $a-b > t-b$, $|L(a-b,t-b)| \le |L_0(a-t)|$. Thus

$$\begin{aligned}&\int_t^U \int_0^t |\pi_\ell(a-b,t-b)||L(a-b,t-b)|\,db\,da \\ &\qquad \le \int_t^T \int_0^t |\pi_\ell(\cdot,t-b)|_\infty |L_0(a-t)|\,db\,da \le C|L_0|_1 \end{aligned} \qquad (2.9)$$

(C is a constant).

From (2.7)–(2.9) we have

$$\begin{aligned}&|I^t(L,M)(\cdot,t)\times(\cdot,\cdot,t)|_1 \\ &\quad \le |L_0|_1 + |M_0|_1 + C|L_0|_1 \\ &\qquad + \int_0^t |\pi_\ell(\cdot,t-b)|_\infty\,|L(\cdot,t-b)|_1\,db + \int_0^t |B(\cdot,t-a)|_\infty |L(\cdot,t-a)|_1\,da \\ &\qquad + \int_0^t |\Gamma(\cdot,\cdot,t-a)|_\infty\,|M(\cdot,\cdot,t-a)|_1\,da \\ &\qquad + \int_0^t \int_0^{t-b} \int_0^k |\pi_m(k,s,t-b)||M(k,s,t-b)|\,ds\,dk\,db \\ &\qquad + \int_0^t \int_{t-b}^T \int_0^k |\pi_m(k,s,t-b)||M(k,s,t-b)|\,ds\,dk\,db\,. \end{aligned} \qquad (2.10)$$

If ${}^t(L,M) \in X_r$, then the right-hand side of (2.10) is bounded in t and hence the left-hand side of (2.10) is in X_r and $I : X_r \to X_r$ is well-defined.

Consider ${}^t(L,M)$ and ${}^t(L^1,M^1)$ in X_r. Note that $I^t(L,M)|_{t=0} = I^t(L^1,M^1)|_{t=0}$. Applying (2.10) we have

$$
\begin{aligned}
&|I^t(L,M)(\cdot,t) \times (\cdot,\cdot,t) - I^t(L^1,M^1)(\cdot,t) \times (\cdot,\cdot,t)|_1 \\
&\quad \le \int_0^t |\pi_\ell(\cdot,t-b)|_\infty |L(\cdot,t-b) - L^1(\cdot,t-b)|_1 \, db \\
&\qquad + \int_0^t |B(\cdot,t-a)|_\infty |L(\cdot,t-a) - L^1(\cdot,t-a)|_1 \, da \\
&\qquad + \int_0^t |\Gamma(\cdot,\cdot,t-a)|_\infty |M(\cdot,\cdot,t-a) - M^1(\cdot,\cdot,t-a)|_1 da \\
&\qquad + \int_0^t \int_0^{U-b} \int_0^k |\pi_m(k,s,t-b)| \\
&\qquad \times |M(k,s,t-b) - M^1(k,s,t-b)| \, ds \, dk \, db \,.
\end{aligned} \tag{2.11}
$$

We examine (2.11)-(2.14) separately.

For (2.11),

$$
\begin{aligned}
&\int_0^t |\pi_\ell(\cdot,t-b)|_\infty |L(\cdot,t-b) - L^1(\cdot,t-b)|_1 \, db \\
&\quad = \int_0^t |\pi_\ell(\cdot,t-b)|_\infty |L(\cdot,t-b) - L^1(\cdot,t-b)|_1 e^{r(t-b)} e^{-r(t-b)} \, db \\
&\quad \le C_1 \|{}^t(L,M) - {}^t(L^1,M^1)\|_{X_r} \int_0^t e^{r(t-b)} \, db \\
&\quad \le C_1 e^{rt} \left(\frac{1}{r}\right) \|{}^t(L,M) - {}^t(L^1,M^1)\|_{X_r} \,.
\end{aligned} \tag{2.12}
$$

By a similar calculation the third and fourth terms in (2.11) are bounded by a similar expression. (2.11) is bounded by

$$
\begin{aligned}
&\int_0^t |\pi_m(\cdot,\cdot,t-b)|_\infty |M(\cdot,\cdot,t-b) - M^1(\cdot,\cdot,t-b)|_1 \, db \\
&\quad = \int_0^t |\pi_m(\cdot,\cdot,t-b)|_\infty |M(\cdot,\cdot,t-b) - M^1(\cdot,\cdot,t-b)|_1 e^{r(t-b)} e^{-r(t-b)} \, db \\
&\quad \le C_1 \|{}^t(L,M) - {}^t(L^1,M^1)\|_{X_r} e^{rt} \left(\frac{1}{r}\right) .
\end{aligned} \tag{2.13}
$$

Together, these estimates show that

$$e^{-rt}|I^t(L,M)(\cdot,t)\times(\cdot,\cdot,t)-I^t(L^1,M^1)(\cdot,t)\times(\cdot,\cdot,t)|_1$$
$$\leq C_2\left(\frac{1}{r}\right)\|^t(L,M)-\ ^t(L^1,M^1)\|_{X_r}\,. \tag{2.14}$$

Hence

$$\|I^t(L,M)-I^t(L^1,M^1)\|_{X_r}\leq C_2\left(\frac{1}{r}\right)\|^t(L,M)-\ ^t(L^1,M^1)\|_{X_r}\,. \tag{2.15}$$

Since C_2 is independent of r, (2.15) shows that for r sufficiently large, $I: X_r \to X_r$ is a strict contraction. Hence it has a unique fixed point in X_r. Since the birth, death and migration coefficients have non-negative entries, for $F \geq 0$, $F \in X_r$, $I(F) \geq 0$ (assuming $L_0, M_0 \geq 0$). Thus the solutions of (1.8), (1.9) have non-negative entries and I is a positive operator in this sense. We summarize the results as

Theorem 2.1. *Equations* (1.8), (1.9) *when* (1.2), (1.3) [*or* (2.4), (2.5)] *are imposed have a unique solution in* X_r *for* r *sufficiently large.* I *is a positive operator on* X_r*. Since* $X_r = X_0$ *as sets for any* $r > 0$*, the result is independent of* r.

3. An Example

An interesting example comes from the species of fish *pollachius virens* (the saithe). The saithe exists in the Northeast Atlantic but we focus on the population known as the West of Scotland Stocks.[5] Some interaction between this population of saithe and the others probably exist, but for the purposes of this example we assume that the population is isolated. This population has a natural geographic division into two locations (patches). Patch A will be the spawning area, (which is a relatively well-defined region west of Scotland along the edge of the continental shelf). Reproduction occurs when adults gather at this spawning ground between February and April. After reproduction, the adults disperse to rebuild biomass (consuming much of their own egg mass in fact). The eggs hatch into a larval stage which apparently disperse via Brownian motion and advection. Only those larvae which move to the coastal waters, which we call patch B, will survive (we assume that this means the coastal waters west of Scotland). Larvae mature to a juvenile stage which stays in coastal regions for about five years (which is age-of-maturity for the saithe). The practical maximum age for the saithe is about 13 years. No patch is ever completely evacuated and the saithe maintains reproductive viability up to maximum age.

In terms of the model, we have the following system:

$$\frac{\partial \ell_A}{\partial t}+\frac{\partial \ell_A}{\partial a}=-\mu_{\ell A}(a,t)\ell_A(a,t)-\pi_{\ell BA}(a,t)\ell_A(a,t)\,, \tag{3.1}$$

$$\ell_B(a,t)\equiv 0 \text{ (no birth happens in patch } B)\,, \tag{3.2}$$

$$\frac{\partial m_A}{\partial t} + \frac{\partial m_A}{\partial b} + \frac{\partial m_A}{\partial a} = -\mu_{mA}(a,b,t)m_A(a,b,t) - \pi_{mBA}(a,b,t)m_A(a,b,t)\,, \quad (3.3)$$

$$\frac{\partial m_B}{\partial t} + \frac{\partial m_B}{\partial b} + \frac{\partial m_B}{\partial a} = -\mu_{mB}(a,b,t)m_B(a,b,t) - \pi_{mAB}(a,b,t)m_B(a,b,t)\,, \quad (3.4)$$

$$\ell_A(0,t) = \int_0^U \beta_A(a,t)\ell_A(a,t)\,da + \int_0^U \int_0^a \gamma_A(a,b,t)m_A(a,b,t)\,db\,da\,, \quad (3.5)$$

$$m_A(a,0,t) = \int_0^a \pi_{mAB}(a,b,t)m_B(a,b,t)\,db\,, \quad (\ell_B = 0)\,, \quad (3.6)$$

$$m_B(a,0,t) = \pi_{\ell BA}(a,t)\ell_A(a,t) + \int_0^a \pi_{mBA}(a,b,t)m_A(a,b,t)\,db\,, \quad (3.7)$$

where μ, π, β, γ are *periodic functions* of time with period one (year). We start the clock at the beginning of reproduction, approximately February 1 in this case.

The length of the reproductive period is called t_1. Migration from A to B also occurs in $[0, t_1]$. $[t_1, t_2]$ is the period spent in B (by adults). $[t_2, 1]$ is the period of migration from B to A.

4. Asymptotic Analysis of the General Model in the Periodic Case

We consider the general conditions imposed in Sec. 2. (See (4.18)–(4.20) below.) We restrict our attention to large time and in addition assume that reproduction is confined to $[0, t_1]$ as in the example (in this case, $t > U$ can be considered large). For $t > U$, (2.4), (2.5) together with (1.8), (1.9) imply

$$\begin{aligned} L(0,t) &= \int_0^U B(a,t)\exp\left(-\int_{t-a}^t \Delta_\ell(s+a-t,s)\,ds\right)L(0,t-a)\,da \\ &\quad + \int_0^U \int_0^a \Gamma(a,b,t)\exp\left(-\int_0^b \Delta_m(a-b+s,s,s+t-b)\right. \\ &\quad \times \left. ds\vphantom{\int} \right) M(a-b,0,t-b)\,db\,da\,, \end{aligned} \quad (4.1)$$

$$\begin{aligned} M(a,0,t) &= \pi_\ell(a,t)\exp\left(-\int_{t-a}^t \Delta_\ell(s+a-t,s)\,ds\right)L(0,t-a) \\ &\quad + \int_0^a \pi_m(a,b,t)\exp\left(-\int_0^b \Delta_m(a-b+s,s,s+t-b)\right. \\ &\quad \times \left. ds\vphantom{\int} \right) M(a-b,0,t-b)\,db\,. \end{aligned} \quad (4.2)$$

To simplify computations, we make the following substitutions:

$$u(t) = L(0,t)\,, \quad (4.3)$$

$$v(a,t) = M(a,0,t)\,, \quad (4.4)$$

$$P_1(a,t) = B(a,t)\exp\left(-\int_{t-a}^{t} \Delta_\ell(s+a-t,s)\,ds\right), \tag{4.5}$$

$$P_2(a,b,t) = \Gamma(a,b,t)\exp\left(-\int_0^b \Delta_m(a-b+s,s,s+t-b)\,ds\right), \tag{4.6}$$

$$q(a,b,t) = \pi_m(a,b,t)\exp\left(-\int_0^b \Delta_m(a-b+s,s,s+t-b)\,ds\right), \tag{4.7}$$

$$r(a,t) = \pi_\ell(a,t)\exp\left(-\int_{t-a}^{t} \Delta_\ell(s+a-t,s)\,ds\right), \tag{4.8}$$

(4.1) and (4.2) can be written as

$$u(t) = \int_0^U P_1(a,t)u(t-a)\,da + \int_0^U \int_0^a P_2(a,b,t)v(a-b,t-b)\,db\,da\,, \tag{4.9}$$

$$v(a,t) = r(a,t)u(t-a) + \int_0^a q(a,b,t)v(a-b,t-b)\,db\,. \tag{4.10}$$

We make the change of variables

$$\tilde{v}(t,s) = v(s,t+s)v(a,t) = \tilde{v}(t-a,a) \tag{4.11}$$

setting $\alpha = t - a$, (4.10) becomes

$$\tilde{v}(\alpha,a) = r(a,\alpha+a)u(\alpha) + \int_0^a q(a,b,\alpha+a)\tilde{v}(\alpha,a-b)\,db\,, \tag{4.12}$$

where Eq. (4.12) is a Volterra equation.

Denote by $\tilde{V}_0(\alpha,a)$ the unique (L^1 matrix) solution to the equation

$$X(\alpha,a) = r(a,\alpha+a) + \int_0^a q(a,b,\alpha+a)X(\alpha,a-b)\,db\,. \tag{4.13}$$

It follows that

$$\tilde{v}(\alpha,a) = \tilde{V}_0(\alpha,a)u(\alpha)\,. \tag{4.14}$$

Inserting (4.14) into (4.9) yields

$$u(t) = \int_0^U P_1(a,t)u(t-a)\,da + \int_0^U \int_0^a P_2(a,b,t)\tilde{V}_0(t-a,a-b)u(t-a)\,db\,da\,. \tag{4.15}$$

If we use the notation

$$W_0(a,t) = P_1(a,t) + \int_0^a P_2(a,b,t)\tilde{V}_0(t-a,a-b)\,db\,, \tag{4.16}$$

then $u(t)$ satisfies the equation

$$u(t) = \int_0^U W_0(a,t)u(t-a)\,da, \quad t > U\,. \tag{4.17}$$

Conversely, solving (4.17) determines $v(a,t)$ for large t; then using (1.8), (1.9), we may compute L and M for large t. Hence (4.17) is equivalent, asymptotically, to the entire system.

To study (4.17) we need further information on W_0. Some elementary properties follow immediately. First, for our example, $P_1(a,t) = P_2(a,b,t) = 0$ for $a < a_0$, (a_0 is the age of maturity). So,

$$W_0(a,t) = 0,\ a < a_0\,. \tag{4.18}$$

In the example, the coefficients are periodic in time with period equal to a year. We will assume this as an extra condition in our general model as follows:

$$\begin{aligned} P_1(a,t+1) &= P_1(a,t)\,,\\ P_2(a,b,t+1) &= P_2(a,b,t)\,,\\ r(a,t+1) &= r(a,t)\,,\\ q(a,b,t+1) &= q(a,b,t)\,. \end{aligned} \tag{4.19}$$

Considering (4.13) we see that $\tilde{V}_0(\alpha+1,a) = \tilde{V}_0(\alpha,a)$ and hence

$$W_0(a,t+1) = W_0(a,t)\,. \tag{4.20}$$

We may write this equation in an instructive way which shows that the system has natural discrete properties and yields important qualitative information. First, we note that (4.17) can be rewritten due to the periodic nature of W_0:

$$u(t) = \sum_{\ell=1}^{U} \int_{\ell-1}^{\ell} W_0(a,t)u(t-a)\,da\,. \tag{4.21}$$

Set $t = k + \tilde{t}$ (recall $t > U$, k is an integer, $0 < \tilde{t} < 1$, in the example $U = 13$) and define $u_k(\tilde{t}) = u(\tilde{t}+k) = u(t), (k > U)$. Note also that $W_0(a,t) = 0$ if $a < a_0$ ($a_0 = 5$ in the example), and the nature of reproduction implies that it occurs only when $\tilde{t} < t_1 < 1$. See Sec. 2 for details.

$$\begin{aligned} u(t) = u_k(\tilde{t}) = \sum_{\ell=a_0}^{U} \Bigg[&\int_{\ell+\tilde{t}-t_1}^{\ell} W_0(a,t)u(t-a)\,da \\ &+ \int_{\ell-1}^{\ell-1+\tilde{t}} W_0(a,t)u(t-a)\,da \Bigg]\,. \end{aligned} \tag{4.22}$$

A change of variable gives (recall also (4.20))

$$u_k(\tilde{t}) = \sum_{\ell=a_0}^{U} \left(\int_{\tilde{t}}^{t_1} W_0(\ell - t_1 + \alpha, \tilde{t}) u_{k-\ell}(\tilde{t} + t_1 - \alpha)\, d\alpha \,. \right.$$

$$\left. + \int_0^{\tilde{t}} W_0(\ell - 1 + \alpha, \tilde{t}) u_{k-\ell+1}(\tilde{t} - \alpha)\, d\alpha \right). \tag{4.23}$$

Another change of variable gives

$$u_k(\tilde{t}) = \int_{\tilde{t}}^{t_1} W_0(U + \tilde{t} - \alpha, \tilde{t}) u_{k-U}(\alpha)\, d\alpha$$

$$+ \sum_{\ell=a_0}^{u-1} \left(\int_{\tilde{t}}^{t_1} W_0(\ell + \tilde{t} - \alpha, \tilde{t} \right) u_{k-\ell}(\alpha)\, d\alpha$$

$$+ \int_0^{\tilde{t}} W_0(\ell - 1 + \tilde{t} - \alpha, \tilde{t}) u_{k+\ell+1}(\alpha)\, d\alpha \,. \tag{4.24}$$

Collecting terms gives

$$u_k(\tilde{t}) = \int_{\tilde{t}}^{t_1} W_0(U + \tilde{t} - \alpha, \tilde{t}) u_{k-U}(\alpha)\, d\alpha$$

$$+ \sum_{\ell=a_0}^{U-1} \int_0^{t_1} W_0(\ell + \tilde{t} - \alpha, \tilde{t}) u_{k-\ell}(\alpha)\, d\alpha \,. \tag{4.25}$$

Introducing the notation $\tilde{W}_\ell(\alpha, \tilde{t}) = W_0(\ell + \tilde{t} - \alpha, \tilde{t})$, Eq. (4.25) reads

$$u_k(\tilde{t}) = \sum_{\ell=a_0}^{U} \int_0^{t_1} \tilde{W}_\ell(\alpha, \tilde{t}) u_{k-\ell}(\alpha)\, d\alpha \,. \tag{4.26}$$

Remark. $\tilde{W}_\ell(\alpha, \tilde{t})$ has a natural interpretation. It gives the instant rate of renewal due to the ℓth age class at the moment α of the reproduction period, $\alpha \in [0, t_1]$.

One can define a discrete dynamical system on the space $Y = L^1(]0, t_1], \mathbb{R}^{NU})$ in terms of the operator K determined by the right-hand side of (3.26):

$$S : (u_1, \ldots, u_U) \to (u_2, u_3, \ldots, u_{U+1})$$

$$u_{U+1}(\tilde{t}) = K(u_1, \ldots, u_U) = \sum \int_0^{t_1} \tilde{W}_\ell(\alpha, \tilde{t}) u(\alpha)\, d\alpha \,. \tag{4.27}$$

It is also convenient to define the following operators

$$R_\ell : \phi \to (R_\ell \phi)(\tilde{t}) = \int_0^{t_1} \tilde{W}_\ell(\alpha, \tilde{t}) \phi(\alpha)\, d\alpha \,. \tag{4.28}$$

Proposition 4.1. *Assume each $\tilde{W}_\ell$ is in $L^\infty(]0,t_1[\times]0,t_1[)$. Then, the map S is eventually compact from Y into Y. More precisely, S^{2U} is compact.*

Proof. Note that each component of the map S^{2U} is a combination of the image of components of $(u_1,\ldots,u_U)$ by the composition of at least two operators R_ℓ.

Claim. For any pair $\ell, m \geq 0$, $R_\ell \cdot R_m$ is a compact operator.

If the claim is true, each component of S^{2U} is a combination of compact operators, therefore, S^{2U} is compact. So, the proof of the proposition will be complete when the claim is proved. The proof of the claim can be done by using arguments on weakly compact maps on L^1.[6] A direct argument is as follows: Let R_1 and R_2 be two kernel operators with essentially bounded kernels. Let us show that $R_2 \cdot R_1$ is compact. □

We have $R_1 : L^1 \to L^\infty$ and is continuous between these two spaces. On the other hand, if we consider the restriction of R_2 to L^∞, $R_2 : L^\infty \to L^1$ is the limit in operator norm of a sequence $R_2^{(n)}$ where each $R_2^{(n)}$ is a kernel operator associated with a continuous function. Such operators are compact from L^∞ into $C([0,t_1])$ (the space of continuous functions). So, R_2 as a uniform limit of compact operators is compact from L^∞ into L^1. Looking now at the product $R_2 \cdot R_1$, we conclude that it is compact.

We will now assume that the $\tilde{W}_\ell$ have a block decomposition in the form

$$\begin{matrix} N_1 & \updownarrow \\ N_2 & \updownarrow \end{matrix} \quad \left[\begin{array}{c|c} \tilde{W}_\ell & 0 \\ \hline 0 & 0 \end{array}\right] = \tilde{W}_\ell \qquad (4.29)$$
$$\qquad\qquad \overleftrightarrow{N_1} \;\; \overleftrightarrow{N_2}$$

(that is N_1, N_2 are block dimensions) which corresponds to the natural assumption that no reproduction takes place in N_2 patches. In the example of the saithe, we know that reproduction takes place in one patch only.

We denote by $u^{(1)}$ the first N_1 components of a vector u,

$$u^{(1)} = (u_1, \ldots, u_{N_1}),$$

and likewise we denote by $T^{(1)}$ the product $\pi_1 \cdot T \cdot i_1$ of any operator T with the canonical embedding i_1 of $\mathbb{R}^{N_1}$ into $\mathbb{R}^N$ and the projection π_1 of $\mathbb{R}^N$ onto $\mathbb{R}^{N_1}$. Our main asymptotic result will be a straightforward consequence of the following spectral properties of the map S. $r(S)$ means the spectral radius of S.

Proposition 4.2. *Suppose there exists $q_0 \geq 1$ such that: for every $q \geq q_0$, and every family $R_{\ell_1}^{(1)} \cdot R_\ell^{(1)}$ has an almost everywhere strictly positive kernel. Then, $r(S) > 0$ is an eigenvalue of S, associated with a strictly positive eigenvector. $r(S)$ has algebraic multiplicity equal to 1, and for any other eigenvalue λ of S we have*

$$|\lambda| < r(S).$$

Remark. Observe that in the proof given below, we actually have that the map S is *primitive* (i.e. some iterate of S is strictly positive). This is stronger than irreducibility. Compare Theorem 4.1 below.

Proof. The proof uses a number of old and new results of the spectral theory of positive operators. For the convenience of the reader, we will give detailed statements of these results. □

As a preliminary, we point out that the assumption made on the products of operators $R^{(1)}$ entails the existence of an integer $q \geq 1$ such that S^q has an almost everywhere strictly positive kernel, i.e.

$$S^q : L^1([0, t_1,], \mathbb{R}^{UN_1}) \to L^1([0, t_1], \mathbb{R}^{UN_1})$$

is determined in terms of a matrix-valued function G,

$$(S^q v)(\bar{t}) = \int_0^{t_1} G(\alpha, \bar{t}) v(\alpha)\, d\alpha \tag{4.30}$$

with each component G_{ij} of G being a.e. positive on the product $]0, t, [\times]0, t_1[$, since positivity entails the property of irreducibility (Definition 4.2.1 of Ref. 7).

Lemma 4.1. (de Pagter's theorem, Theorem 4.2.2 of Ref. 7) *If T is a positive compact irreducible operator on a Banach lattice X, then $r(T)$, the spectral radius of T, is positive ($r(T) > 0$). The same conclusion holds if instead of T being compact it is assumed that some iterate T^k is compact.*

Lemma 4.2. (Krein–Rutman theorem, Theorem 4.1.4 of Ref. 7) *Let T be a positive operator with a compact iterate, on a Banach lattice X. Assume that $r(T) > 0$. Then, $r(T)$ is an eigenvalue of T, corresponding to a positive eigenvector. Also, $r(T^*) = r(T) \in \sigma(T^*)$ and T^* has a positive eigenvector for this value.*

Corollary. *Let T be a positive irreducible operator with compact iterate. Then, $r(T) > 0$ is an eigenvalue of T corresponding to a positive eigenvector, $v; r(T)$ is also an eigenvalue of T^* and has a positive eigenvector v^* for this value. Moreover, v and v^* are such that:*

$$x^*(v) > 0\,, \quad \textit{for every } x^* > 0\,, \tag{4.31}$$

and

$$v^*(x) > 0\,, \quad \textit{for every } x > 0\,. \tag{4.32}$$

Finally, $r(T)$ has algebraic multiplicity equal to one.

We will now restrict our attention to a kernel operator, that is we assume that T is defined on a space $X = L^1(J, \mathbb{R}^N)$, where J is a finite interval of $\mathbb{R}$ and T is defined by a matrix-valued function K as

$$(T\varphi)(x) = \int_J K(x, y)\varphi(y)\, dy, \quad x \in J\,. \tag{4.33}$$

We assume that all the components of K are a.e. positive on $J \times J$ and bounded. In view of the proof of Proposition 4.1, we conclude that T is compact.

It is also irreducible. So, the corollary applies and yields $r(T) > 0$, $r(T)$ is an eigenvalue of T and has a positive eigenvector v. Likewise, T^* has a positive eigenvector v^* for the same eigenvalue; $r(T)$ has algebraic multiplicity one and v and v^* verify (4.31) and (4.32).

Definition 4.1.[7] For a bounded linear operator T, the peripheral spectrum of T is the set

$$\sigma_0(T) = \{\lambda \in \sigma(T) : |\lambda| = r(T)\}.$$

At this point, applying the above results to the operator S, all the results stated in Proposition 4.2 can be concluded except for the fact that any other eigenvalue λ of T is such that: $|\lambda| < r(T)$. We will prove this fact now. The result can be formulated in terms of the peripheral spectrum. It amounts to showing that $\sigma_0(T) = \{r(T)\}$.

Lemma 4.3. *Let T be a positive operator on X, with kernel K such that all the components of K are strictly positive and K is bounded. Then, $\sigma_0(T) = \{r(T)\}$.*

Proof. Assume that there exists $\alpha \in \sigma_0(T)$, $|\alpha| = r(T)$; w being an eigenvector for that eigenvalue. We denote by $|w|$, the vector function defined by

$$|w| = (|w_1|, \dots, |w_N|),$$

where $|w_j|(x) = |w_j(x)|$, for all $x \in J$. Clearly, we have

$$T(|w|) \geq r(T)|w|.$$

Assuming that $T(|w|) \neq r(T)|w|$ and multiplying the above inequality by v^* on both sides we obtain, in view of (4.32), (write r for $r(T)$)

$$v^*(T(|w|)) > rv^*(|w|),$$

a contradiction since

$$v^*(T(|w|)) = (T^*v^*)|w| = rv^*(|w|).$$

So, we have $T(|w|) = r|w|$, which implies, due to the fact that the multiplicity of r is one, $|w| = v$, i.e. $w_j = v_j g_j$, where $|g_j(x)| = 1$, for all $x \in J, j \in \{1, \dots, N\}$. So, we have

$$|T((v_j g_j)_{j<j\leq N})| = Tv,$$

which in componentwise gives

$$\left| \int_J \sum_k K_{jk}(x,y) v_k(y) g_k(y)\, dy \right| = \int_J \sum_k K_{jk}(x,y) v_k(y)\, dy.$$

This equality holds a.e.

Let x be a point where it holds. We can rewrite the absolute value in the form

$$\int_J e^{i\theta}\left(\sum_k K_{jk}(x,y)v_k(y)g_k(y)\right)dy = \int_J \sum_k K_{jk}(x,y)v_k(y)\,dy\,,$$

which implies

$$\int_J \operatorname{Re}\left(e^{i\theta}\sum_k K_{jk}(x,y)v_h(y)g_k(y)\right)dy = \int_J \sum_k K_{jk}(x,y)v_k(y)\,dy\,,$$

for some θ depending only on x. So,

$$\operatorname{Re}\left(e^{i\theta}\sum_k K_{jk}(x,y)v_k(y)g_k(y)\right) = \sum_k K_{jk}(x,y)v_k(y)\,,$$

$$\Rightarrow \operatorname{Re}(e^{i\theta}g_k(y)) = 1 \text{ a.e. in } y\,.$$

With $|g_k(y)| = 1$ for all y, the above relation yields

$$g_k(y) = e^{-i\theta}\,, \quad \text{a.e. in } y, \text{ for all } k\,.$$

We obtain that

$$w = e^{-i\theta}v\,,$$

$$Tw = e^{-i\theta}Tv = r(T)w\,.$$

Again $\alpha = r(T)$ and $\sigma(T) = \{r(T)\}$, which completes the proof of Lemma 3. □

The assumption of Proposition 4.2 has the following consequence. There exists $q_0 \geq 0$ such that for every $q \geq q_0$, S^q has an almost everywhere strictly positive kernel. Applying the corollary to the operator S we conclude that $r(S) > 0$ is an eigenvalue of S with algebraic multiplicity equal to one, corresponding to a positive eigenvector. Lemma 3 implies that $\sigma_0(S^q) = \{r(S)^q\}$, for every $q \geq q_0$, thus

$$\sigma_0(S) = \{r(S)\}\,,$$

which completes the proof of Proposition 4.2.

We will now deduce the consequences of Proposition 4.2 regarding the asymptotic behavior of the solutions of the system (1.2)–(1.5). Let us first give an expression of the eigenvector corresponding to $r(S)$.

For notational convenience, write r for $r(S)$. If $u = (u_r, \ldots, u_U)$ is an eigenvector of S for the eigenvalue r, we have in view of (4.27),

$$u_2 = ru_1, \ldots, u_{U+1} = ru_U = \cdots = r^U u_1\,,$$

and

$$r^U u_1(\tilde{t}) = \sum_{\ell=5}^{U} \int_0^{t_1} \tilde{W}_\ell(\alpha,\tilde{t})r^{U-\ell}u_1\,d\alpha\,.$$

Dividing by r^U we obtain the following fixed point equation:

$$u_1(\tilde{t}) = \sum_{\ell=5}^{U} \int_0^{t_1} \tilde{W}_\ell(\alpha, \tilde{t}) r^{-\ell} u_1(\alpha)\, d\alpha\,. \tag{4.34}$$

Define

$$H(r, \alpha, \tilde{t}) = \sum_{\ell=5}^{U} r^{-\ell} \tilde{W}_\ell(\alpha, \tilde{t})\,, \tag{4.35}$$

and denote by $\mathcal{H}(r)$ the map from $L^1([0, t_1], \mathbb{R}^{N_1})$ into itself defined by

$$\mathcal{H}(r)(\phi)(\tilde{t}) = \int_0^{t_1} H(r, \alpha, \tilde{t}) \phi(\alpha)\, d\alpha\,. \tag{4.36}$$

It is easily seen that $\mathcal{H}(r)$ is a positive operator, with a compact iterate and the conditions stated in Proposition 4.2 imply that $\mathcal{H}(r)$ is irreducible. In particular, we have

$$\sum_{\ell=5}^{U} \int_0^{t_1} \tilde{W}_\ell(\alpha, \tilde{t})\, d\alpha \gg 0$$

for all $\tilde{t} \in]0, t_1[$. But, irreducibility entails more properties. From the comparison property

$$\mathcal{H}(r_1) > \mathcal{H}(r_2) \text{ for } r_1 < r_2$$

we deduce that $r(\mathcal{H}(r))$ is decreasing in r with: $r(\mathcal{H}(r)) \to +\infty$ as $r \to 0$ and $r(\mathcal{H}(r)) \to 0$ as $r \to +\infty$.

So, there is exactly one value of r for which $r(\mathcal{H}(r)) = 1$. The spectral properties of the operator S established in Proposition 4.2 can be investigated through the operator $\mathcal{H}(r)$ and in fact the conclusion of Proposition 4.2 can be reached under slightly weaker assumptions than those made in Proposition 4.2. We state the results as follows.

Theorem 4.1. *We assume that the functions $\tilde{W}_\ell$ are non-negative and bounded. Moreover, we assume that for all $p \geq p_1$, the operator $(\mathcal{H}(1))^p$ has an a.e. strictly positive kernel. Then, the same is true for all $\mathcal{H}(r), r > 0$. For every $r > 0$, $r(\mathcal{H}(r)) > 0$ is an eigenvalue of $\mathcal{H}(r)$ associated with a strictly positive eigenvector, $r(\mathcal{H}(r))$ has algebraic multiplicity equal to one and for any other eigenvalue λ of $\mathcal{H}(r)$, we have*

$$|\lambda| < r(\mathcal{H}(r))\,.$$

Finally, there is exactly one value of r, say r^*, $0 < r^* < +\infty$, for which

$$r(\mathcal{H}(r^*)) = 1\,.$$

Compared to Proposition 4.2, the above result does not assume strict positivity of the product $R^{(1)}_{\ell_1}, \ldots, R^{(1)}_{\ell}$ for $p \geq p_0$. Only a certain iterate of the sum of all the R_{ℓ_i} has a strictly positive kernel.

Regarding the asymptotic behavior of the iterates of S, the results are the same as in the case of Proposition 4.2. In fact, for each eigenvalue λ of S, $\lambda \neq r^*$, it is easily seen that

$$1 \in \sigma(\mathcal{H}(\lambda)),$$

and this implies

$$|\lambda| < r^*.$$

One can also show by considering the expression

$$1 \in \sigma(\mathcal{H}(\lambda))$$

that r^* has algebraic multiplicity equal to one as an eigenvalue of S. So, if we denote by ϕ, a positive fixed point of $\mathcal{H}(r^*)$ and

$$\Psi = (\phi, r^*\phi, \ldots, r^{*U-1}\phi),$$

there exists $\varepsilon > 0$ and for each

$$u \in \left(L^1(]0, t_1[, \mathbb{R}^{N_1 U})\right),$$

there exists C, such that

$$S^j U = \left(C r^{*j}\Psi + O((r^* - \varepsilon)^j)\right).$$

In particular, we have

$$u_j(\tilde{t}) = C r^{*j}\phi(\tilde{t}) + O((r^* - \varepsilon)^j).$$

Moreover, $C > 0$ if $u > 0$.

In terms of the original variable t, this yields

$$u(t) = u_{[t]}(t - [t]) = C r^{*[t]}\phi(t - [t]) + O((r^* - \varepsilon)^{[t]})$$
$$u(t) = C r^{*t}\{r^{*[t]-t}\phi(t - [t])\} + O((r^* - \varepsilon)^t).$$

So, $u(t)$, the vector of birth rates at time t, has a principal part of the form

$$C e^{\lambda^* t}\mathcal{B}(t),$$

where $\lambda^* = \ln(r^*)$ and $\mathcal{B}$ is the periodic function with period one defined by

$$\mathcal{B}(t) = (r^{*-t})\phi(t), \text{ for } 0 < t < 1.$$

In order to determine the asymptotic expression of v, we first compute v in terms of $\tilde{v}$ using (4.11) and (4.19): $v(a,t) = \tilde{v}(t - a, a)$ (in view of (4.11)) which, thanks to (4.19) yields

$$v(a,t) = \tilde{V}_0(t - a, a) < u(t - a).$$

Formulas (4.7), (4.8) and (4.13) show that $\tilde{V}_0(t-a,a)$ is periodic in t, with period one. We arrive at an expression of the form

$$v(a,t) = Ce^{\lambda^* t}\mathcal{M}(a,t) + O(e^{(\lambda^*-\eta)t}),$$

where $\mathcal{M}$ is periodic in t with period one, for some $\eta > 0$.

From the assumption made on the structure of the $\tilde{W}_\ell$ (Eq. (4.29)), the functions $\mathcal{B}(t)$ and $\mathcal{M}(a,t)$ have the first N_1 components positive and the last N_2 components equal to zero. The same is true for the last N_2 components of the respective remainders of $u(t)$ and $v(a,t)$. Coming back to the original variables, we obtain an asymptotic expression for both the newborns and the new immigrants:

$$\begin{cases} L(0,t) = e^{\lambda^* t}(C\mathcal{B}(t) + O(e^{-\eta t})) \\ M(a,0,t) = e^{\lambda^* t}(C\mathcal{M}(a,t) + O(e^{-\eta t})). \end{cases}$$

Using Eqs. (1.8) and (1.9) with $t > a$ we obtain asymptotic formulas for $L(a,t)$ and $M(a,b,t)$. The only change with the formulas for $L(0,t), M(a,0,t)$ are multiplications by periodic functions with period one.

Application to the saithe model

We now return to the example introduced in Sec. 2. We briefly describe the functions corresponding to this case.

This is a model with two patches: patch A (the spawning area) and patch B (the nurseries). So, $N = 2$.

We have

$$B(a,t) = \operatorname{diag}(\beta_A(a,t), 0),$$

$$\Gamma(a,b,t) = \operatorname{diag}(\gamma_A(a,b,t), 0),$$

$$\Delta_{\ell_A}(a,t) = \mu_{\ell A}(a,t) + \mu_{BA}(a,t),$$

$$\Delta_\ell(a,t) = \operatorname{diag}(\Delta_{\ell_A}(a,t), 0),$$

$$\Delta_{mA}(a,b,t) = \mu_{mA}(a,b,t) + \pi_{mBA}(a,b,t),$$

$$\Delta_{mB}(a,b,t) = \mu_{mB}(a,b,t) + \pi_{mAB}(a,b,t),$$

$$\Delta_m(a,b,t) = \operatorname{diag}(\Delta_{mA}, \Delta_{MB}),$$

$$P_1(a,t) = \operatorname{diag}\left(\beta_A(a,t)\exp - \int_{t-a}^{t} \Delta_{\ell_A}(s+a-t,s)\,ds, 0\right),$$

$$P_2(a,b,t) = \operatorname{diag}\left(\gamma_A(a,b,t)\exp - \int_0^b \Delta_{m_A}(a-b+s,s+t-b)\,ds, 0\right),$$

$$\pi_\ell(a,t) = \begin{pmatrix} 0 & 0 \\ \pi_{\ell_{BA}(a,t)} & 0 \end{pmatrix},$$

$$\pi_m(a,b,t) = \begin{pmatrix} 0 & \pi_{m_{AB}}(a,b,t) \\ \pi_{m_{BA}}(a,b,t) & 0 \end{pmatrix},$$

$$q(a,b,t) = \begin{pmatrix} 0 & \begin{array}{l} \pi_{m_{BA}}(a,b,t)\exp \\ -\int_0^b \Delta_{m_A}(a-b+s, s_t - b)\,ds \end{array} \\ \begin{array}{l} \pi_{m_{AB}}(a,b,t)\exp \\ -\int_0^b \Delta_{m_B}(a-b+s, s+t-b)\,dx \end{array} & 0 \end{pmatrix},$$

$$r(a,t) = \begin{pmatrix} 0 & 0 \\ \pi_{\ell_{BA}}(a,t)\Delta_{\ell_A}(a,t) & 0 \end{pmatrix}.$$

Using the above expressions, we can compute the function $\tilde{V}_0(\alpha, a)$, by solving the fixed point Eq. (4.13), and from the computation of $\tilde{V}_0$, we obtain W_0 according to formula (4.16). It is easily seen that $\tilde{V}_0$ is of the form $\begin{pmatrix} + & 0 \\ + & 0 \end{pmatrix}$ and W_0 is of the form $\begin{pmatrix} + & 0 \\ 0 & 0 \end{pmatrix}$. Here, we have: $N_1 = N_2 = 1$. "The + indicates that the entry is positive." A sufficient condition on the coefficients of the equation for the hypotheses of Theorem 4.1 to hold is that $B_A(a,t) > 0$ for $a \geq 5$, $\ell < t < \ell + t_1$ for every $\ell \geq 0$. This means that persistence of a population in patch A is sufficient to ensure ergodicity of the whole population (with respect to the age structure).

A possible set of conditions is that:

$$r_{2,1}(a, \alpha + a) > 0\,, \quad 0 < a < \frac{1}{3}\,, \quad \text{and } \frac{2}{3} < \alpha < 1\,,$$

$$q_{1,2}(a,b,2+\alpha) > 0, \quad 0 < a - b < \frac{1}{3}, a > 5, \frac{2}{3} < \alpha < 1\,,$$

with the birthrate of migrants $\gamma_A(a,b,t) > 0$, for every $\ell < t < \ell + t_1$, $\ell \geq 0$, $a \geq 5$, $b < a$.

Fish populations are examples where migratory effects play an essential role in general. Most fish are born in some place where adults meet during the reproduction season, and mature in other places, the nurseries. Many species are also subject to migration within the water column: from the pelagic stage as larvae, they become benthic species as juveniles and adults. What sorts of movements are involved? There are marine currents, tidal currents, there are movements provoked by gradients of temperature, there is also a random motion in search of food. Fish are also moving to escape from predators, they are also engaged in group motions (shoals of fish). This makes a variety of causes of movement and it is very difficult to model individual motion, although such models have been proposed (e.g., Refs. 2 and 7). The model presented in this paper tends to overlook the transient periods when the fish are actually traveling between two specific areas. It only takes into consideration the time spent in a given area and models the transition rates between two areas as a function of age, time spent and chronological time. Under quite general conditions on the coefficients (essentially, positivity during some time periods) it has been shown that the population verifies the ergodic property: all age classes tend to represent a strictly positive fixed fraction of the total population. The model does not take fishing into account. Our future work will be concerned with introducing compensatory effects inside the population, still without fishing, and will focus on the existence and stability of a positive equilibrium.

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