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A Model of an Age-Structured Population in a Multipatch Environment

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Abstract—We propose a model of an age-structured population divided into N geographical patches. We distinguish two time scales, at the fast time scale we have the migration dynamics and at the slow time scale the demographic dynamics. The demographic process is described using the classical McKendrick-von Foerster model for each patch, and a simple matrix model including the transfer rates between patches depicts the migration process.

Assuming that 0 is a simple strictly dominant eigenvalue for the migration matrix, we transform the model (an e.d.p. problem with N state variables) into a classical McKendrick-von Foerster model (scalar e.d.p. problem) for the global variable: total population density. We prove, under certain assumptions, that the semigroup associated to our problem has the property of positive asynchronous exponential growth and so we compare its asymptotic behaviour to that of the transformed scalar model. This type of study can be included in the so-called aggregation methods, where a large scale dynamical system is approximately described by a reduced system. Aggregation methods have been already developed for systems of ordinary differential equations and for discrete time models.

An application of the results to the study of the dynamics of the Sole larvae is also provided.

Keywords—Approximate aggregation of variables, Population dynamics, Time scales, Dynamical systems.

1. INTRODUCTION

Aggregation methods study the relationship between a large class of complex systems and their corresponding "aggregated" systems. The aim of aggregation methods is two fold. First of all, the simpler aggregated systems summarize the dynamics of the complex ones, allowing their analytical study, and second, the complex systems justify the form of the aggregated ones. The property of complex systems that allows their aggregation is the existence of two different time scales. The reduced system, or aggregated system, must reflect in a certain way both dynamics, the one corresponding to the fast time scale and the one corresponding to the slow time scale. The aggregation methods have already been developed in the case of systems of ordinary differential equations with different time scales, see [1–4], and in the case of time discrete systems, see [5–7].

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The aim of this work is to extend these methods to the case of some partial differential equations used when modelling age-structured populations in continuous time. Models for the continuous time dynamics of populations structured by continuous structuring variables can be described by means of mass balance equations [8] which, in simpler cases, take the form of the so-called McKendrick-von Foerster equation [9,10]. In these models, the population is described by means of a density distribution (per unit of the structuring variable), which as a function of time and the structuring variable, satisfies a first-order hyperbolic partial differential equation. This equation accounts for transitions out of and between structuring classes, under the assumption that the population is closed to immigration and emigration and suffers losses only through death, modeled by the per capita death rate. In the McKendrick-von Foerster model, births are modeled by a boundary condition of integral type involving the age-specific per capita birth rate.

The interest of aggregation in the mentioned setting has appeared in the modelization of the dynamics of a Sole population. The life cycle of the Sole of Bay of Biscay has been intensively studied in the field as well as in laboratory [11,12]. Recently, a theoretical approach has taken account of the main features of the dynamics of the Sole population [13]. The life cycle of Sole is divided into four stages: eggs, larvae, juveniles, and adults. The model proposed by Arino *et al.* [13] takes as state variables the densities of the four stages as functions of time, age (structuring variable), and a special variable (distance from the coast). Nevertheless, it seems to be important to take account of the daily migrations of larvae towards the surface after sunset and towards the sea bed before sunrise. This is so because of the different predation rates depending on the depth (to be included in the mortality rate) and also because of the selective tidal stream transport at the surface. In the present work, we include the influence of depth in the demography of larvae by dividing the water column into several spatial patches with different mortality rates.

In Section 2, we present a model of an age-structured population divided into N spatial patches that distinguishes two time scales. The fast dynamics represents the migration process between patches, and it is considered linear and age independent. The slow dynamics describes the demography process by means of the McKendrick-von Foerster model with different mortality and fertility rates for every patch. Assuming that the fast dynamics reaches constant equilibrium frequencies in every patch, we build up an aggregated model which is a classical McKendrick-von Foerster model. The asymptotic behaviour of the aggregated model is then well known. Sections 3 and 4 study the asymptotic behaviour of the initial model and compare it to that of the aggregated model. The main result of the work states that both models have the property of positive asynchronous exponential growth, with the dominant eigenvalue of the initial model approximating that of the aggregated one, and with the dominant eigenfunction of the initial model approximating that of the aggregated one times the vector of equilibrium frequencies of the fast dynamics. Finally, Section 5 applies this result to the demography of a population of sole larvae considered divided into four spatial patches representing four different depth areas in the column water.

2. THE MODEL

We consider an age-structured population, with age a and time t being continuous variables. The population is divided into N spatial patches. The evolution of the population is due to the migration process between the different patches at a fast time scale, and to the demographic process at a slow time scale.

We denote by $n_i(a,t)$ the population density in patch i ($i = 1, \dots, N$), so that $\int_{a_1}^{a_2} n_i(a,t)\,da$ represents the number of individuals in patch i whose age $a \in [a_1, a_2]$ at time t. Let $\mu_i(a)$ and $\beta_i(a)$ be the mortality and fertility rates, respectively, and $k_{ij}(a)$ the migration rate from patch j to patch i, $i \neq j$. The evolution of the population is described in a standard way (see [14]) as follows.

Balance law:

$$\frac{\partial n_i}{\partial a} + \frac{\partial n_i}{\partial t} = -\mu_i(a) n_i + R\left(\sum_{j=1}^{N} k_{ij}(a) n_j - \sum_{j=1}^{N} k_{ji}(a) n_i\right), \tag{1}$$

$a > 0$, $t > 0$, $i = 1, \dots, N$, where $R > 0$ is a big enough constant which describes the fact that the migration process evolves at a fast time scale compared to the demographic process.
Birth law:

$$n_i(0,t) = \int_0^{+\infty} \beta_i(a) n_i(a,t)\, da, \tag{2}$$

$t > 0$, $i = 1, \dots, N$.
Initial age distribution:

$$n_i(a,0) = \phi_i(a), \tag{3}$$

$a > 0$, $i = 1, \dots, N$.

Using the next notation,

$$\mathbf{n}(a,t) = (n_1(a,t), \dots, n_N(a,t))^\top,$$
$$\mathbf{M}(a) = \mathrm{diag}\{\mu_1(a), \dots, \mu_N(a)\}, \qquad \mathbf{B}(a) = \mathrm{diag}\{\beta_1(a), \dots, \beta_N(a)\},$$
$$\mathbf{K}(a) = (k_{ij}(a))_{1 \le i,j \le N},$$

with $k_{ii}(a) = -\sum_{j=1, j\neq i}^{N} k_{ji}(a)$ and

$$\phi(a) = (\phi_1(a), \dots, \phi_N(a))^\top,$$

we write systems (1)–(3) in matrix form.
Balance law:

$$\frac{\partial \mathbf{n}}{\partial a} + \frac{\partial \mathbf{n}}{\partial t} = [-\mathbf{M}(a) + R\mathbf{K}(a)]\mathbf{n}(a,t), \tag{4}$$

$a > 0$, $t > 0$.
Birth law:

$$\mathbf{n}(0,t) = \int_0^{+\infty} \mathbf{B}(a)\mathbf{n}(a,t)\, da, \tag{5}$$

$t > 0$.
Initial age distribution:

$$\mathbf{n}(a,0) = \phi(a), \tag{6}$$

$a > 0$.

2.1. Aggregated Model

We pretend to build up a model for the evolution of the so-called global variable

$$n(a,t) = \sum_{i=1}^{N} n_i(a,t).$$

First of all, we notice that the exact model the global variable satisfies can be obtained adding up from $i = 1$ to N in systems (1)–(3):

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\sum_{i=1}^{N} \mu_i(a) n_i(a,t), \qquad (a > 0,\ t > 0), \tag{7}$$

$$n(0,t) = \int_0^{+\infty} \left(\sum_{i=1}^{N} \beta_i(a), n_i(a,t)\right) da, \qquad (t > 0), \tag{8}$$

$$n(a,0) = \phi(a) = \sum_{i=1}^{N} \phi_i(a), \qquad (a > 0). \tag{9}$$

Above, we have taken account in (7) of the fact that the elements of every column of matrix $\mathbf{K}(a)$ sum up to 0, reflecting the invariance of the global variable n through the migration process. That is, we neglect the demographic process then the global variable is constant along the time.

It is obvious, nevertheless, that systems (7)–(9) still depend on the variables n_i, while our aim is to find an aggregated, or global, model for the global variable n. To get it we suppose henceforth that matrix $\mathbf{K}(a) = \mathbf{K}$ is age independent. The matrix $\mathbf{K}$ has nonnegative coefficients off its main diagonal. This kind of matrices are called ML-matrices [15]. Moreover, 0 is one of its eigenvalues. And furthermore, we assume that $\mathbf{K}$ is irreducible, a hypothesis that ensures the existence of an asymptotically stable equilibrium of the fast dynamics (migration process) for each value of n. We summarize the hypothesis made on $\mathbf{K}$.

HYPOTHESIS H1. *The matrix* $\mathbf{K}$ *is an irreducible* ML*-matrix.*

Assuming H1, 0 is a simple eigenvalue of $\mathbf{K}$, and the rest of its eigenvalues have negative real part. The left eigenspace of matrix $\mathbf{K}$ associated to the eigenvalue 0 is generated by vector $\mathbf{1} = (1, \dots, 1)^\top \in \mathbf{R}^N$, and the right eigenspace is generated by vector $\boldsymbol{\nu}$ that we choose having positive entries and verifying $\mathbf{1}^\top \boldsymbol{\nu} = 1$.

In systems (7)–(9), we propose the following approximation:

$$\nu_i(a,t) = \frac{n_i(a,t)}{n(a,t)} \approx \nu_i, \qquad (i = 1, \dots, N),$$

and that yields

$$\sum_{i=1}^{N} \mu_i(a) n_i(a,t) \approx \left(\sum_{i=1}^{N} \mu_i(a) \nu_i \right) n(a,t) = \mu^*(a) n(a,t),$$

where

$$\mu^*(a) = \sum_{i=1}^{N} \mu_i(a) \nu_i = \mathbf{1}^\top \mathbf{M}(a) \boldsymbol{\nu} \tag{10}$$

and

$$\sum_{i=1}^{N} \beta_i(a) n_i(a,t) \approx \left(\sum_{i=1}^{N} \beta_i(a) \nu_i \right) n(a,t) = \beta^*(a) n(a,t),$$

where

$$\beta^*(a) = \sum_{i=1}^{N} \beta_i(a) \nu_i = \mathbf{1}^\top \mathbf{B}(a) \boldsymbol{\nu}. \tag{11}$$

So, we have built up an approximated model for the global density of the population, which we call aggregated system:

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu^*(a) n(a,t), \qquad (a > 0,\ t > 0), \tag{12}$$

$$n(0,t) = \int_0^{+\infty} \beta^*(a) n(a,t)\, da, \qquad (t > 0), \tag{13}$$

$$n(a,0) = \phi(a), \qquad (a > 0). \tag{14}$$

The aggregated model we have obtained is the classical McKendrick-von Foerster model, where the mortality and fertility rates $\mu^*(a)$ and $\beta^*(a)$ take account of both the equilibria of the migration process and the rates of the demographic process, as it is easily noticed from (10) and (11).

2.2. Asymptotic Behaviour of the Aggregated Model

The asymptotic behaviour of the aggregated systems (12)–(14) will be studied using well-known results of semigroup theory [14]. The necessary assumptions to be made on μ_j and β_j, $j = 1, \ldots, N$ are summarized in the next two hypotheses.

HYPOTHESIS H2.

$$\mu_j \in L^\infty(\mathbf{R}_+), \qquad j = 1, \ldots, N,$$

and moreover, there exists $\eta > 0$ so that

$$\inf_{a \in \mathbf{R}_+} \mu^*(a) = \inf_{a \in \mathbf{R}_+} \mathbf{1}^\top \mathbf{M}(a) \boldsymbol{\nu} \geq \eta.$$

HYPOTHESIS H3.

$$\beta_j \in L^1(\mathbf{R}_+), \qquad j = 1, \ldots, N,$$

and moreover, there exists $\alpha \in \mathbf{R}$ so that

(i) $\limsup_{a \to +\infty} e^{\alpha a} \|\mathbf{B}(a)\| < +\infty$,

(ii) $\int_0^{+\infty} e^{\alpha a} \beta^*(a) e^{-\int_0^a \mu^*(s)\, ds}\, da > 1$.

Assuming H2 and H3, problems (12)–(14) have an associated strongly continuous semigroup of linear operators $\{T(t)\}_{t \geq 0}$ on $L^1(\mathbf{R}_+)$, so that, for $t \geq 0$, $T(t)\phi = n(\cdot, t)$ is the solution corresponding to the initial age distribution ϕ. This semigroup is positive and its infinitesimal generator is the operator

$$A\varphi = -\varphi' - \mu^*(\cdot)\varphi,$$

with domain

$$D(A) = \left\{ \varphi \in L^1(\mathbf{R}_+);\ \varphi' \in L^1(\mathbf{R}_+);\ \varphi(0) = \int_0^{+\infty} \beta^*(a)\varphi(a)\, da \right\}.$$

As usual, the asymptotic behaviour of the semigroup $\{T(t)\}_{t \geq 0}$ can be studied from the spectrum $\sigma(A)$ of its infinitesimal generator. The equation $(A - \lambda I)\varphi = 0$ gives nontrivial solutions $\varphi \in D(A)$ if and only if λ is a solution of the characteristic equation

$$1 = \int_0^{+\infty} e^{-\lambda a} e^{-\int_0^a \mu^*(s)\, ds} \beta^*(a)\, da. \tag{15}$$

Because of Hypothesis H3, there exists a unique $\lambda^* \in \mathbf{R}$ which is solution of (15), and verifying also $\lambda^* > -\alpha$. The semigroup $\{T(t)\}_{t \geq 0}$ then has the property of asynchronous exponential growth that we state in the following proposition.

PROPOSITION 1. Let H1, H2, and H3 hold. If $n(a, t)$ is the solution of problems (12)–(14) corresponding to the initial age distribution $\phi \in L^1(\mathbf{R}_+)$, there exists a constant $C(\phi)$ such that

$$\lim_{t \to +\infty} e^{-\lambda^* t} n(a, t) = C(\phi) e^{-\lambda^* a - \int_0^a \mu^*(s)\, ds},$$

where λ^* is the only real solution of (15) and the limit is taken in the L^1 norm.

In the next sections, we compare the asymptotic behaviours of the solutions of (1)–(3) to that of the solutions of the aggregated model.

3. STABLE AGE DISTRIBUTIONS OF THE MODEL

Starting from systems (4)–(6), we change the big constant R by $1/\varepsilon$ and study the existence of solutions with the next form:

$$\mathbf{n}(a,t) = e^{\lambda t}\varphi(a).$$

Substituting in (4),(5) and making $\varphi_\lambda(a) = e^{\lambda a}\varphi(a)$, we obtain

$$\varphi_\lambda'(a) = -\mathbf{M}(a)\varphi_\lambda(a) + \frac{1}{\varepsilon}\mathbf{K}\varphi_\lambda(a), \tag{16}$$

$$\varphi_\lambda(0) = \int_0^{+\infty} e^{\lambda a}\mathbf{B}(a)\varphi_\lambda(a)\, da. \tag{17}$$

We begin the study of the dependence on ε of the solution φ_λ. The Hypothesis H1 allows us to write the following direct sum decomposition:

$$\mathbf{R}^N = [\boldsymbol{\nu}] \oplus S,$$

where $[\boldsymbol{\nu}]$ is the eigenspace of matrix $\mathbf{K}$ associated to the eigenvalue 0 and

$$S = \left\{\mathbf{v} \in \mathbf{R}^N;\ \mathbf{1}^\top\mathbf{v} = 0\right\},$$

so the restriction of $\mathbf{K}$ to the subspace S, that we call $\mathbf{K}_S$, is an isomorphism on S and its spectrum $\sigma(\mathbf{K}_S) \subset \{\lambda \in \mathbf{C};\ \mathrm{Re}\,\lambda < 0\}$.

According to the last decomposition, we can write

$$\varphi_\lambda(a) = \theta_\lambda(a)\boldsymbol{\nu} + \boldsymbol{\sigma}_\lambda(a), \qquad \boldsymbol{\sigma}_\lambda(a) \in S, \quad a > 0.$$

If we substitute this last expression in (16), premultiply by $\mathbf{1}^\top$ to project on $[\boldsymbol{\nu}]$ and call $\mathbf{M}_S(a)$ to the projection of $\mathbf{M}(a)$ on S, we obtain the following equations for the components of the decomposition of $\varphi_\lambda(a)$:

$$\theta_\lambda'(a) = -\mu^*(a)\theta_\lambda(a) - \mathbf{1}^\top\mathbf{M}(a)\boldsymbol{\sigma}_\lambda(a), \tag{18}$$

$$\boldsymbol{\sigma}_\lambda'(a) = \left[\frac{1}{\varepsilon}\mathbf{K}_S - \mathbf{M}_S(a)\right]\boldsymbol{\sigma}_\lambda(a) - \theta_\lambda(a)\mathbf{M}_S(a)\boldsymbol{\nu}. \tag{19}$$

LEMMA 1. *Let $R_\varepsilon(a,\alpha)$, $a \geq \alpha$, with $R_\varepsilon(\alpha,\alpha) = I$, be the resolvent matrix of the homogeneous system*

$$\boldsymbol{\sigma}_\lambda'(a) = \left[\frac{1}{\varepsilon}\mathbf{K}_S - \mathbf{M}_S(a)\right]\boldsymbol{\sigma}_\lambda(a).$$

There exist constants $k_1 > 0$, $k_2 > 0$, and $k_3 > 0$ such that

$$\|R_\varepsilon(a,\alpha)\| \leq k_3 e^{(k_2 - k_1/\varepsilon)(a-\alpha)}, \qquad a \geq \alpha. \tag{20}$$

PROOF. See the Appendix.

With the help of $R_\varepsilon(a,\alpha)$, we can write the next expression for $\boldsymbol{\sigma}_\lambda(a)$:

$$\boldsymbol{\sigma}_\lambda(a) = R_\varepsilon(a,0)\boldsymbol{\sigma}_\lambda(0) - \int_0^a R_\varepsilon(a,\alpha)\mathbf{M}_S(\alpha)\boldsymbol{\nu}\theta_\lambda(\alpha)\, d\alpha,$$

and substituting in (18), we obtain

$$\theta_\lambda'(a) = -\mu^*(a)\theta_\lambda(a) + \int_0^a r_\varepsilon(a,\alpha)\theta_\lambda(\alpha)\, d\alpha - \mathbf{1}^\top\mathbf{M}(a)R_\varepsilon(a,0)\boldsymbol{\sigma}_\lambda(0),$$

where we have used the notation

$$r_\varepsilon(a,\alpha) = \mathbf{1}^\top \mathbf{M}(a) R_\varepsilon(a,\alpha)\mathbf{M}_S(\alpha)\boldsymbol{\nu}.$$

Let us notice that

$$|r_\varepsilon(a,\alpha)| \le k_4 e^{(k_2-k_1/\varepsilon)(a-\alpha)}, \qquad a \ge \alpha.$$

LEMMA 2. *Let $\rho_\varepsilon(a,\alpha)$, $a \ge \alpha$, with $\rho_\varepsilon(\alpha,\alpha) = I$, be the resolvent of the homogeneous integro-differential equation*

$$\theta'_\lambda(a) = -\mu^*(a)\theta_\lambda(a) + \int_\alpha^a r_\varepsilon(a,\beta)\theta_\lambda(\beta)\,d\beta.$$

For $0 < \varepsilon < \varepsilon_0$, there exists a constant $C > 0$ such that

$$|\rho_\varepsilon(a,\alpha)| \le \frac{K_M}{K_M + \varepsilon C}\left[e^{-K_M(a-\alpha)} + \frac{\varepsilon C}{K_M} e^{\varepsilon C(a-\alpha)}\right], \qquad a \ge \alpha,$$

where K_M is any positive constant such that $K_M < \inf_{a\ge 0}\mu^*(a)$.

PROOF. See the Appendix.

With the help of this last resolvent $\rho_\varepsilon(a,\alpha)$, we can finally write the solution of the equations (18),(19) and obtain the following expressions for the components $\theta(a)$, $\boldsymbol{\sigma}(a)$ of the solution $\boldsymbol{\varphi}(a)$ of equation (16):

$$\theta(a) = e^{-\lambda a}\rho_\varepsilon(a,0)\theta(0) + e^{-\lambda a}\boldsymbol{\xi}_\varepsilon^\top(a)\boldsymbol{\sigma}(0),$$
$$\boldsymbol{\sigma}(a) = e^{-\lambda a}\boldsymbol{\eta}_\varepsilon(a)\theta(0) + e^{-\lambda a}\boldsymbol{\Lambda}_\varepsilon(a)\boldsymbol{\sigma}(0),$$

where we have used the next notations:

$$\boldsymbol{\xi}_\varepsilon^\top(a) = \int_0^a \rho_\varepsilon(a,\alpha)\mathbf{1}^\top\mathbf{M}(\alpha)R_\varepsilon(\alpha,0)\,d\alpha,$$
$$\boldsymbol{\eta}_\varepsilon(a) = \int_0^a R_\varepsilon(a,\alpha)\mathbf{M}_S(\alpha)\boldsymbol{\nu}\rho_\varepsilon(\alpha,0)\,d\alpha,$$
$$\boldsymbol{\Lambda}_\varepsilon(a) = R_\varepsilon(\alpha,0) + \int_0^a R_\varepsilon(a,\alpha)\mathbf{M}_S(\alpha)\boldsymbol{\nu}\boldsymbol{\xi}_\varepsilon^\top(a)\,d\alpha.$$

The expression we have obtained for $\boldsymbol{\varphi}(a) = \theta(a)\boldsymbol{\nu} + \boldsymbol{\sigma}(a)$ must also verify the birth equation

$$\boldsymbol{\varphi}(0) = \int_0^{+\infty} \mathbf{B}(a)\boldsymbol{\varphi}(a)\,da,$$

or decomposed

$$\theta(0)\boldsymbol{\nu} + \boldsymbol{\sigma}(0) = \left(\int_0^{+\infty} \mathbf{B}(a)\theta(a)\,da\right)\boldsymbol{\nu} + \int_0^{+\infty}\mathbf{B}(a)\boldsymbol{\sigma}(a)\,da.$$

Projecting on the subspaces $[\boldsymbol{\nu}]$ and S, and through some straightforward calculations, we can write:

$$\theta(0) = d_1(\varepsilon,\lambda)\theta(0) + \mathbf{d}_2^\top(\varepsilon,\lambda)\boldsymbol{\sigma}(0),$$
$$\boldsymbol{\sigma}(0) = \mathbf{d}_3(\varepsilon,\lambda)\theta(0) + \mathbf{D}_4(\varepsilon,\lambda)\boldsymbol{\sigma}(0),$$

with

$$d_1(\varepsilon,\lambda) = \int_0^{+\infty}\beta^*(a)e^{-\lambda a}\rho_\varepsilon(a,0)\,da + \int_0^{+\infty}\mathbf{1}^\top\mathbf{B}(a)\boldsymbol{\eta}_\varepsilon(a)e^{-\lambda a}\,da,$$
$$\mathbf{d}_2^\top(\varepsilon,\lambda) = \int_0^{+\infty}\beta^*(a)e^{-\lambda a}\boldsymbol{\xi}_\varepsilon^\top(a)\,da + \int_0^{+\infty}\mathbf{1}^\top\mathbf{B}(a)\boldsymbol{\Lambda}_\varepsilon(a)e^{-\lambda a}\,da,$$
$$\mathbf{d}_3(\varepsilon,\lambda) = \int_0^{+\infty}e^{-\lambda a}\rho_\varepsilon(a,0)\mathbf{B}_S(a)\boldsymbol{\nu}\,da + \int_0^{+\infty}e^{-\lambda a}\mathbf{B}_S(a)\boldsymbol{\eta}_\varepsilon(a)\,da,$$
$$\mathbf{D}_4(\varepsilon,\lambda) = \int_0^{+\infty}e^{-\lambda a}\mathbf{B}_S(a)\boldsymbol{\Lambda}_\varepsilon(a)\,da + \int_0^{+\infty}e^{-\lambda a}\mathbf{B}_S(a)\boldsymbol{\nu}\boldsymbol{\xi}_\varepsilon^\top(a)\,da,$$

where $\mathbf{B}_S(a)$ is the projection of $\mathbf{B}(a)$ on S.

The last system must have nontrivial solutions $\theta(0), \boldsymbol{\sigma}(0)$, hence the eigenvalue λ_ε associated to the solution $\mathbf{n}(a,t) = e^{\lambda_\varepsilon t}\varphi(a)$ is a solution of the characteristic equation

$$\det \begin{pmatrix} d_1(\varepsilon,\lambda) - 1 & \mathbf{d}_2^\top(\varepsilon,\lambda) \\ \mathbf{d}_3(\varepsilon,\lambda) & \mathbf{D}_4(\varepsilon,\lambda) - \mathbf{I} \end{pmatrix} = 0. \tag{21}$$

The main result of this work is that problems (4)–(6) have the property of asynchronous exponential growth, and moreover, when $\varepsilon \to 0$ (analogously $R \to \infty$) this asymptotic behaviour is approximating the asymptotic behaviour of the aggregated system stated in Proposition 1.

The first step toward completing our task is proving the existence of real solutions of the characteristic equation (21) in any neighbourhood of the eigenvalue λ^* which leads the asymptotic behaviour of the aggregated system. To prove that, we need the following lemma.

LEMMA 3.

$$\lim_{\varepsilon \to 0_+} \rho_\varepsilon(a,0) = \rho_0(a,0),$$

uniformly for $a \geq 0$, *where*

$$\rho_0(a,0) = e^{-\int_0^a \mu^*(s)\,ds}.$$

PROOF. See the Appendix.

It follows immediately from the lemma that there exists $\varepsilon_0 > 0$ such that $\rho_\varepsilon(a,0) > 0$, $(a \geq 0)$ holds for every $\varepsilon < \varepsilon_0$.

PROPOSITION 2. *For every* $\delta > 0$, *there exists* $\varepsilon_0(\delta) > 0$ *such that for every* $0 < \varepsilon < \varepsilon_0(\delta)$ *the characteristic equation (21) possesses at least a real solution* $\lambda_\varepsilon^* \in [\lambda^* - \delta, \lambda^* + \delta]$.

PROOF. It is easy to prove that for a fixed $\delta > 0$, we have that

$$\sup_{\lambda > \lambda^* - \delta_0} \|\mathbf{D}_4(\varepsilon,\lambda)\| \longrightarrow 0, \qquad (\varepsilon \to 0_+),$$

and then $\mathbf{I} - \mathbf{D}_4(\varepsilon,\lambda)$ is invertible for every $\lambda > \lambda^* - \delta_0$ and $0 < \varepsilon < \varepsilon_0$, for some $\varepsilon_0 > 0$ small enough. Hence,

$$\boldsymbol{\sigma}_\varepsilon(0) = (\mathbf{I} - \mathbf{D}_4(\varepsilon,\lambda))^{-1}\mathbf{d}_3(\varepsilon,\lambda)\theta_\varepsilon(0),$$

and substituting it in the expression of $\theta_\varepsilon(0)$, since we are looking for nontrivial solutions of $\theta_\varepsilon(0)$ and $\boldsymbol{\sigma}_\varepsilon(0)$, we can reduce the characteristic equation (21) to

$$1 = \int_0^{+\infty} \beta^*(a) e^{-\lambda a} \rho_\varepsilon(a,0)\,da + \sigma(\varepsilon,\lambda),$$

where

$$\sigma(\varepsilon,\lambda) = \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \boldsymbol{\eta}_\varepsilon(a) e^{-\lambda a}\,da + \mathbf{d}_2^\top(\varepsilon,\lambda)(\mathbf{I} - \mathbf{D}_4(\varepsilon,\lambda))^{-1}\mathbf{d}_3(\varepsilon,\lambda),$$

and it holds that

$$\sup_{\lambda > \lambda^* - \delta_0} |\sigma(\varepsilon,\lambda)| \longrightarrow 0, \qquad (\varepsilon \to 0_+).$$

From Lemma 3, it follows that

$$\rho_\varepsilon(a,0) = e^{-\int_0^a \mu^*(s)\,ds} + g(\varepsilon,a), \quad \sup_{a \geq 0} |g(\varepsilon,a)| \longrightarrow 0, \qquad (\varepsilon \to 0_+),$$

and then

$$1 = \int_0^{+\infty} \beta^*(a) e^{-\lambda a} e^{-\int_0^a \mu^*(s)\,ds}\,da + \tilde{\sigma}(\varepsilon,\lambda), \tag{22}$$

with

$$\tilde{\sigma}(\varepsilon,\lambda) = \int_0^{+\infty} \beta^*(a)e^{-\lambda a}g(\varepsilon,a)\,da + \sigma(\varepsilon,\lambda), \qquad \sup_{\lambda>\lambda^*-\delta_0} |\tilde{\sigma}(\varepsilon\,\lambda)| \longrightarrow 0, \qquad (\varepsilon \to 0_+).$$

From Hypothesis H3, for any fixed $0 < \delta < \delta_0$, there exists $\tilde{\varepsilon}_0(\delta) > 0$ such that if $0 < \varepsilon < \tilde{\varepsilon}_0(\delta)$, then

$$G(\varepsilon, \lambda^* - \delta) > 1 > G(\varepsilon, \lambda^* + \delta),$$

where we have called $G(\varepsilon, \lambda)$ the second member of (22).

Then, for any fixed small enough ε, there exists $\lambda_\varepsilon^* \in [\lambda^* - \delta, \lambda^* + \delta]$ such that $G(\varepsilon, \lambda_\varepsilon^*) = 1$. This λ_ε is a real root of the characteristic equation (21).

LEMMA 4. *Let $\varphi_\varepsilon(a)$ be the eigenfunction associated to the eigenvalue λ_ε^*. Then,*

$$\lim_{\varepsilon\to 0_+} \varphi_\varepsilon(a) = \theta^*(a)\boldsymbol{\nu}, \qquad a \geq 0,$$

where

$$\theta^*(a) = e^{-\lambda^* a - \int_0^a \mu^*(s)\,ds}$$

is the age distribution associated to the asymptotic behaviour of the aggregated model.

PROOF. See the Appendix.

4. ASYMPTOTIC BEHAVIOUR OF THE MODEL

Problems (1)–(3) define in the usual way, for every $\varepsilon > 0$, a strongly continuous semigroup of bounded linear operators on the space $L^1(\mathbf{R}_+, \mathbf{R}^N)$, which we call $\{U_\varepsilon(t)\}_{t\geq 0}$. We have then, for every $\phi \in L^1(\mathbf{R}_+, \mathbf{R}^N)$,

$$U_\varepsilon(t)\phi = \mathbf{n}_\varepsilon(\cdot, t),$$

where $\mathbf{n}_\varepsilon$ is the solution of (1)–(3) corresponding to the initial age distribution ϕ. From Hypothesis H1 and the properties of the classical McKendrick-von Foerster model, it follows that the semigroup $\{U_\varepsilon(t)\}_{t\geq 0}$ is positive and irreducible. Its infinitesimal generator is

$$A_\varepsilon\varphi = -\varphi' - \left[\mathbf{M}(\cdot) - \frac{1}{\varepsilon}\mathbf{K}\right]\varphi,$$

with domain

$$D(A_\varepsilon) = \left\{\varphi \in L^1\left(\mathbf{R}_+, \mathbf{R}^N\right);\ \varphi' \in L^1\left(\mathbf{R}_+, \mathbf{R}^N\right);\ \varphi(0) = \int_0^\infty \mathbf{B}(a)\varphi(a)\,da\right\}.$$

From Proposition 2, it follows that $\sigma(A_\varepsilon) \neq \emptyset$ and then, using the general theory (see [16,17]), $s(A_\varepsilon) \in \sigma(A_\varepsilon)$, where $s(A_\varepsilon) = \sup\{\operatorname{Re}\lambda; \lambda \in \sigma(A_\varepsilon)\}$. In particular, $s(A_\varepsilon) \geq \lambda_\varepsilon^*$.

Lemma 4 implies that, for $\varepsilon > 0$ small enough, $\varphi_\varepsilon(a) > 0$, $a \geq 0$, and, moreover, $\varphi_\varepsilon(a)$ is an eigenvector of the infinitesimal generator A_ε associated to the eigenvalue λ_ε^*.

On the other hand, it is well known that the eigenvalue $s(A_\varepsilon)$ has an associated eigenvalue which is positive. $s(A_\varepsilon)$ is also an eigenvalue of the adjoint operator A_ε^* and has an associated eigenvalue which is positive also, denoted by ω_ε^*.

We have then

$$A_\varepsilon\varphi_\varepsilon = \lambda_\varepsilon^*\varphi_\varepsilon \quad \text{and} \quad A_\varepsilon^*\omega_\varepsilon^* = s(A_\varepsilon)\omega_\varepsilon^*,$$

and denoting $\langle\cdot,\cdot\rangle$ the product in the usual duality, we obtain

$$\langle A_\varepsilon^*\omega_\varepsilon^*, \varphi_\varepsilon\rangle = s(A_\varepsilon)\langle\omega_\varepsilon^*, \varphi_\varepsilon\rangle,$$
$$\langle A_\varepsilon^*\omega_\varepsilon^*, \varphi_\varepsilon\rangle = \langle\omega_\varepsilon^*, A_\varepsilon\varphi_\varepsilon\rangle = \lambda_\varepsilon^*\langle\omega_\varepsilon^*, \varphi_\varepsilon\rangle,$$

but $\langle\omega_\varepsilon^*, \varphi_\varepsilon\rangle \neq 0$, which implies that $s(A_\varepsilon) = \lambda_\varepsilon^*$.

THEOREM. *Let H1, H2, and H3 hold. For every $\varepsilon > 0$ small enough, if $\mathbf{n}_\varepsilon(a,t)$ is the solution of problems (1)–(3) corresponding to the initial age distribution $\phi \in L^1(\mathbf{R}_+, \mathbf{R}^N)$, there exists a constant $C_\varepsilon(\phi)$ such that*

$$\lim_{t\to+\infty} e^{-\lambda_\varepsilon^* t}\mathbf{n}_\varepsilon(a,t) = C_\varepsilon(\phi)\varphi_\varepsilon(a),$$

where λ_ε^* is the unique real solution of the characteristic equation (21) and φ_ε is the associated positive eigenfunction.

Moreover, $\lim_{\varepsilon\to 0_+} \lambda_\varepsilon^* = \lambda^*$, where λ^* is the unique real solution of (15), and $\lim_{\varepsilon\to 0_+} \varphi_\varepsilon(a) = \theta^*(a)\boldsymbol{\nu}$.

5. APPLICATION TO A SOLE LARVAE POPULATION

In this section, we apply the result of Section 4 to a model that describes some aspects of the dynamics of a sole population at its larval stage. For a detailed study of the life cycle of the sole of Biscay Bay, see [11,12]. In our model, we avoid the horizontal movements towards the coast included in a general model developed in [13] but, on the other hand, we depict the daily vertical migrations of sole larvae by distinguishing five depth zones as [11] does when taking field data. The fact that the process of vertical migration is daily allows us to consider it as a fast process compared to the demographic process which takes some months to be completed.

Let $n_i(a,t)$ be the population density of sole larvae in patch i, $i = 1,2,3,4,5$. Let $\mu_i(a)$ and $\beta_i(a)$ be the mortality and fertility rates, respectively. The migration matrix $\mathbf{K}$ has the next form:

$$\begin{pmatrix} -k_{21} & k_{12} & 0 & 0 & 0 \\ k_{21} & -(k_{12}+k_{32}) & k_{23} & 0 & 0 \\ 0 & k_{32} & -(k_{23}+k_{43}) & k_{34} & 0 \\ 0 & 0 & k_{43} & -(k_{34}+k_{54}) & k_{45} \\ 0 & 0 & 0 & k_{54} & -k_{45} \end{pmatrix},$$

and it is easy to see that an eigenvector of $\mathbf{K}$ associated to its eigenvalue 0 is

$$\mathbf{v} = [v_1, v_2, v_3, v_4, v_5] = [k_{12}k_{23}k_{34}k_{45},\ k_{23}k_{34}k_{45}k_{21},\ k_{34}k_{45}k_{32}k_{21},\ k_{45}k_{43}k_{32}k_{21},\ k_{54}k_{43}k_{32}k_{21}],$$

hence, the normalized vector $\boldsymbol{\nu}$ of equilibrium frequencies is

$$\boldsymbol{\nu} = \frac{1}{v_1+v_2+v_3+v_4+v_5}\mathbf{v}.$$

The model is

$$\begin{aligned} \frac{\partial \mathbf{n}}{\partial a} + \frac{\partial \mathbf{n}}{\partial t} &= [-\mathbf{M}(a) + R\mathbf{K}]\mathbf{n}(a,t), && (a>0,\ t>0), \\ \mathbf{n}(0,t) &= \int_0^{+\infty} \mathbf{B}(a)\mathbf{n}(a,t)\,da, && (t>0), \\ \mathbf{n}(a,0) &= \phi(a), && (a>0), \end{aligned}$$

where

$$\mathbf{M}(a) = \begin{pmatrix} \mu_1(a) & 0 & 0 & 0 & 0 \\ 0 & \mu_2(a) & 0 & 0 & 0 \\ 0 & 0 & \mu_3(a) & 0 & 0 \\ 0 & 0 & 0 & \mu_4(a) & 0 \\ 0 & 0 & 0 & 0 & \mu_5(a) \end{pmatrix},$$

and

$$\mathbf{b}(a) = \begin{pmatrix} \beta_1(a) & 0 & 0 & 0 & 0 \\ 0 & \beta_2(a) & 0 & 0 & 0 \\ 0 & 0 & \beta_3(a) & 0 & 0 \\ 0 & 0 & 0 & \beta_4(a) & 0 \\ 0 & 0 & 0 & 0 & \beta_5(a) \end{pmatrix}.$$

With the precisions made in the theorem of Section 5, we know that the asymptotic behaviour of our model could be approximated by the following expression:

$$C(\phi)e^{\lambda^* t}e^{-\lambda^* a-\int_0^a \mu^*(s)\,ds}\boldsymbol{\nu},$$

where $\mu^*(a) = \mu_1(a)\nu_1 + \mu_2(a)\nu_2 + \mu_3(a)\nu_3 + \mu_4(a)\nu_4 + \mu_5(a)\nu_5$, and λ^* is the unique real solution of the equation

$$1 = \int_0^{+\infty} e^{-\lambda a}e^{-\int_0^a \mu^*(s)\,ds}\beta^*(a)\,da,$$

with $\beta^*(a) = \beta_1(a)\nu_1 + \beta_2(a)\nu_2 + \beta_3(a)\nu_3 + \beta_4(a)\nu_4 + \beta_5(a)\nu_5$.

6. CONCLUSION

In the present work, we have established the relationship between the asymptotic behaviour of an age-structured model in a multipatch environment and its aggregated model, a classical McKendrick-von Foerster model. This approach can be generalized to models structured by other stage different from age. In the application of Section 5, we conclude from our results that the vertical migrations of the sole larvae could be included approximately in a scalar model by a sort of averaging of the fertility and mortality rates by means of the equilibrium frequencies of the migration process. This kind of result justifies, to a certain extent, the fact of neglecting the vertical migrations in order to simplify the model. In the future, we intend to obtain the same type of results when the migration matrix is age and/or time dependent, and when the slow dynamics not only represents the demographic process, but also diffusion and transport processes.

APPENDIX

PROOF OF LEMMA 1

From $\sigma(\mathbf{K}|_S) \subset \{\lambda \in \mathbf{C};\ \mathrm{Re}\,\lambda < 0\}$, we deduce the existence of a symmetric positive definite matrix $\mathbf{Q}$ such that

$$\mathbf{K}_S^\top\mathbf{Q} + \mathbf{Q}\mathbf{K}_S = -\mathbf{I}.$$

We define $w(a) = \boldsymbol{\sigma}_\lambda^\top(a)\mathbf{Q}\boldsymbol{\sigma}_\lambda(a)$ and notice that there exist positive constants C_1 and C_2 which verify

$$C_1 w(a) \le \|\boldsymbol{\sigma}_\lambda(a)\|^2 \le C_2 w(a). \tag{23}$$

We also have

$$w'(a) = -\frac{1}{\varepsilon}\|\boldsymbol{\sigma}_\lambda(a)\|^2 - \boldsymbol{\sigma}_\lambda^\top(a)[\mathbf{M}_S(a)^\top\mathbf{Q} + \mathbf{Q}\mathbf{M}_S(a)]\boldsymbol{\sigma}_\lambda(a).$$

Then, it follows from Hypothesis H2 and inequality (23) that

$$w'(a) \le \left(k_2 - \frac{k_1}{\varepsilon}\right) w(a),$$

which yields

$$w(a) \le w(a)e^{(k_2-k_1/\varepsilon)(a-\alpha)}, \qquad a \ge \alpha,$$

and hence,

$$\|\boldsymbol{\sigma}_\lambda(a)\|^2 \le k_3\|\boldsymbol{\sigma}_\lambda(a)\|^2 e^{(k_2-k_1/\varepsilon)(a-\alpha)}, \qquad a \ge \alpha.$$

From that, it follows immediately the stated inequality for the resolvent $R_\varepsilon(a,\alpha)$.

PROOF OF LEMMA 2

We know that $\rho_\varepsilon(a,\alpha)$ is the solution of the problem

$$v'(a) = -\mu^*(a)v(a) + \int_\alpha^a r_\varepsilon(a,\beta)v(\beta)\,d\beta,$$
$$v(\alpha) = 1,$$

whose expression is

$$v(a) = e^{-\int_\alpha^a \mu^*(s)\,ds} + \int_\alpha^a v(\beta)\left(\int_\beta^a e^{-\int_s^a \mu^*(u)\,du} r_\varepsilon(s,\beta)\,ds\right)d\beta.$$

From inequality (20), it follows that there exists a positive constant C such that

$$\left|\int_\beta^a e^{-\int_s^a \mu^*(u)\,du} r_\varepsilon(s,\beta)\,ds\right| \le \varepsilon C,$$

for $\varepsilon > 0$ small enough, and hence,

$$v(a) \le e^{-K_M(a-\alpha)} + C\varepsilon \int_\alpha^a v(\beta)\,d\beta,$$

that can be written by making $w(p) = v(p+\alpha)$ and $p = a - \alpha$ in the next form

$$w(p) - C\varepsilon \int_0^p w(s)\,ds \le e^{-K_M p}, \tag{24}$$

which implies that

$$\frac{d}{dp}\left[e^{-C\varepsilon p}\int_0^p w(s)\,ds\right] \le e^{-C\varepsilon p}e^{-K_M p}.$$

Integrating both members, we obtain

$$\int_0^p w(s)\,ds \le \frac{e^{-\varepsilon C p} - e^{-K_M p}}{K_M + \varepsilon C}.$$

The proof of the lemma is finished by substituting the last inequality in (24).

PROOF OF LEMMA 3

We write

$$\rho_\varepsilon(a,0) = e^{-\int_0^a \mu^*(s)\,ds} f_\varepsilon(a),$$

and obtain the next equation for f_ε:

$$f_\varepsilon'(a) = \int_0^a r_\varepsilon(a,\beta)e^{\int_\beta^a \mu^*(s)\,ds} f_\varepsilon(\beta)\,d\beta,$$
$$f_\varepsilon(0) = 1.$$

Integrating in $[0,a]$

$$f_\varepsilon(a) = 1 + \int_0^a d\alpha\left[\int_0^\alpha r_\varepsilon(\alpha,\beta)e^{\int_\beta^\alpha \mu^*(s)\,ds} f_\varepsilon(\beta)\,d\beta\right]. \tag{25}$$

Let us consider, for $\gamma > 0$, the space

$$E_\gamma = \left\{f \in C(\mathbf{R}_+);\ |f(a)| \le Ce^{\gamma a}, a \ge 0\right\},$$

which is a Banach space with the following norm:

$$\|f\|_\gamma = \sup_{a\geq 0} |f(a)|e^{-\gamma a}.$$

For every $\varepsilon > 0$, we define the operator $K_\varepsilon : E_\gamma \to E_\gamma$

$$(K_\varepsilon f)(a) = \int_0^a d\alpha \left[\int_0^\alpha r_\varepsilon(\alpha,\beta) e^{\int_\beta^\alpha u^*(s)\,ds} f(\beta)\,d\beta\right].$$

After some straightforward computations where it is necessary to use inequality (20) and Hypothesis H2, we obtain

$$\|K_\varepsilon f\|_\gamma = \sup_{a\geq 0} |(K_\varepsilon f)(a)|e^{-\gamma a} \leq \varepsilon C_1 \|f\|_\gamma \left[\frac{1}{\gamma} + \frac{\varepsilon}{C_2}\right],$$

where C_1 and C_2 are positive constants and ε is small enough. Now we have, for fixed $\gamma > 0$, there exists $\varepsilon_0(\gamma) > 0$ such that for every $\varepsilon \in [0, \varepsilon_0(\gamma)]$ the following inequality holds:

$$\|K_\varepsilon\|_\gamma < 1. \tag{26}$$

Equation (25) can be written in the form

$$f_\varepsilon(a) = 1 + (K_\varepsilon f_\varepsilon)(a),$$

and also,

$$((I - K_\varepsilon) f_\varepsilon)(a) = 1.$$

From (26) it follows, for a fixed $\gamma > 0$, that the operator $I - K_\varepsilon$ is invertible in E_γ for small enough $\varepsilon > 0$, and that yields the existence of a unique solution $f_\varepsilon \in E_\gamma$.

Now, we can write

$$\rho_\varepsilon(a,0) = e^{-\int_0^a \mu^*(s)\,ds} f_\varepsilon(a) = \rho_0(a,0)(1 + (K_\varepsilon f_\varepsilon)(a)),$$

and hence,

$$\begin{aligned}\sup_{a\geq 0} |\rho_\varepsilon(a,0) - \rho_0(a,0)| &\leq \sup_{a\geq 0} e^{-\int_0^a \mu^*(s)\,ds} |(K_\varepsilon f_\varepsilon)(a)| \\ &\leq \sup_{a\geq 0} e^{-\gamma a} |(K_\varepsilon f_\varepsilon)(a)| = \|K_\varepsilon f_\varepsilon\|_\gamma \to 0, \qquad (\varepsilon \to 0_+),\end{aligned}$$

where the constant $\gamma > 0$ is anyone verifying the Hypothesis H2. The last inequality completes the proof of lemma.

PROOF OF LEMMA 4

We have

$$\varphi_\varepsilon(a) = \theta_\varepsilon(a)\boldsymbol{\nu} + \boldsymbol{\sigma}_\varepsilon(a),$$

where

$$\begin{aligned}\theta_\varepsilon(a) &= e^{-\lambda_\varepsilon^* a}\rho_\varepsilon(a,0)\theta_\varepsilon(0) + e^{-\lambda_\varepsilon^* a}\boldsymbol{\xi}_\varepsilon^\top(a)\boldsymbol{\sigma}_\varepsilon(0), \\ \boldsymbol{\sigma}_\varepsilon(a) &= e^{-\lambda_\varepsilon^* a}\boldsymbol{\eta}_\varepsilon(a)\theta_\varepsilon(0) + e^{-\lambda_\varepsilon^* a}\boldsymbol{\Lambda}_\varepsilon(a)\boldsymbol{\sigma}_\varepsilon(0).\end{aligned}$$

We can choose $\theta_\varepsilon(0) = 1$, and then it is easy to obtain

$$\lim_{\varepsilon\to 0} \boldsymbol{\sigma}_\varepsilon(0) = \int_0^{+\infty} e^{-\lambda^* a}\rho_0(a,0)\mathbf{B}_S(a)\boldsymbol{\nu}\,da.$$

Hence, for a fixed $a \geq 0$, it is verified that

$$\begin{aligned}&\lim_{\varepsilon\to 0} \boldsymbol{\sigma}_\varepsilon(a) = \mathbf{0}, \\ &\lim_{\varepsilon\to 0} \theta_\varepsilon(a) = e^{-\lambda^* a}\rho_0(a,0) = \theta^*(a).\end{aligned}$$

The last equalities complete the proof of the lemma.

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