



A Model for an Age-Structured Population with Two Time Scales

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Abstract—In the modelisation of the dynamics of a sole population, an interesting issue is the influence of daily vertical migrations of the larvae on the whole dynamical process. As a first step towards getting some insight on that issue, we propose a model that describes the dynamics of an age-structured population living in an environment divided into N different spatial patches. We distinguish two time scales: at the fast time scale, we have migration dynamics and at the slow time scale, the demographic dynamics. The demographic process is described using the classical McKendrick model for each patch, and a simple matrix model including the transfer rates between patches depicts the migration process. Assuming that the migration process is conservative with respect to the total population and some additional technical assumptions, we proved in a previous work that the semigroup associated to our problem has the property of positive asynchronous exponential growth and that the characteristic elements of that asymptotic behaviour can be approximated by those of a scalar classical McKendrick model. In the present work, we develop the study of the nature of the convergence of the solutions of our problem to the solutions of the associated scalar one when the ratio between the time scales is ε ($0 < \varepsilon \ll 1$). The main result decomposes the action of the semigroup associated to our problem into three parts:

- (1) the semigroup associated to a demographic scalar problem times the vector of the equilibrium distribution of the migration process;
- (2) the semigroup associated to the transitory process which leads to the first part; and
- (3) an operator, bounded in norm, of order ε .

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1. INTRODUCTION

Many fish, especially flatfish, spawn offshore but early juveniles develop inshore and several mechanisms may be involved in the transport of larval and early juvenile stages from spawning grounds to nurseries. In the case of the sole, *Solea solea*, active vertical migrations are involved during the larval stage, see [1,2]. These migrations are provoked by light; the lack of light is followed by upward movements and vice versa. Thus, the process of vertical migration is performed daily, which is a fast time scale in comparison with that of the demographic process. From a theoretical point of view, Arino *et al.* [3] proposed a model which takes account of the main features of the dynamics of the Sole population of the Bay of Biscay. Nevertheless, they did not observe the daily migrations of larvae.

In [4], the authors proposed a model which includes the influence of vertical migrations in the demography of larvae. It is 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 independent of age, the slow dynamics describes the demographic process by means of the McKendrick model with different age-specific mortality and fertility rates for every patch. The existence of two time scales suggests the extension of the aggregation methods, already developed in discrete models of structured populations (see [5,6]), to the present case where time and age are continuous variables. Models for the continuous time dynamics of populations structured by continuous structuring variables can be described by means of mass balance equations [7], which, in simpler cases, assume the form of the McKendrick equation.

Aggregation methods, as well as other reduction methods, associate to a system where two processes are acting at different time scales a reduced system. This aggregated system is obtained by supposing that the fast process instantaneously attains its equilibrium. A second task of the method is to determine the distance between the results obtained from the reduced system and the real ones. In [4], an aggregated system has been constructed which is associated to the initial one by assuming that the fast dynamics reaches constant equilibrium frequencies in every patch. The initial and the aggregated systems (a classical McKendrick model) share the property of positive asynchronous exponential growth, with their dominant eigenvalues close enough. Moreover, the dominant eigenfunction of the initial system is approximated by the product of the dominant eigenfunction of the aggregated one and the vector of equilibrium frequencies of the fast dynamics.

The aim of this work is to complete the study of the model presented in [4]. From a mathematical point of view the model is a linear system of partial differential equations where the state variables are the population densities in each spatial patch, together with a boundary condition of integral type, the birth equation. Due to the two different time scales, the system depends on a small parameter ε and can be thought of as a singular perturbation problem. We study the nature of the convergence of the approximate solutions obtained through the aggregated system towards the real solutions of the model when ε tends to zero. The parameter ε could be interpreted as the time needed for a single patch migration.

2. THE MODEL

We consider an age-structured population, with continuous age a and time t . 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.

Let $n_i(a, t)$ be 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 with age $a \in [a_1, a_2]$ at time t , and

$$\mathbf{n}(a, t) = (n_1(a, t), \dots, n_N(a, t))^T.$$

Let $\mu_i(a)$ and $\beta_i(a)$ be the patch and age-specific mortality and fertility rates, respectively, and

$$\mathbf{M}(a) = \text{diag}\{\mu_1(a), \dots, \mu_N(a)\}, \quad \mathbf{B}(a) = \text{diag}\{\beta_1(a), \dots, \beta_N(a)\}.$$

Let k_{ij} be the migration rate from patch j to patch i , $i \neq j$, and

$$\mathbf{K} = (k_{ij})_{1 \leq i, j \leq N},$$

with $k_{ii} = -\sum_{j=1, j \neq i}^N k_{ji}$.

The model based upon the classical McKendrick model for an age-structured population reads as follows.

Balance Law

$$\frac{\partial \mathbf{n}}{\partial a} + \frac{\partial \mathbf{n}}{\partial t} = \left[-\mathbf{M}(a) + \frac{1}{\varepsilon} \mathbf{K} \right] \mathbf{n}(a, t), \quad (a > 0, t > 0), \quad (1)$$

where $0 < \varepsilon \ll 1$ describes the fact that the migration process evolves at a fast time scale compared to the demographic process.

Birth Law

$$\mathbf{n}(0, t) = \int_0^\infty \mathbf{B}(a) \mathbf{n}(a, t) da, \quad (t > 0). \quad (2)$$

Initial Age Distribution

$$\mathbf{n}(a, 0) = \phi(a), \quad (t > 0). \quad (3)$$

The matrix \mathbf{K} has nonnegative off-diagonal elements and the sum of its columns is equal to zero. If we assume that \mathbf{K} is irreducible, then Theorem 2.6 of [8, pp. 46–47] applies and we have that 0 is a simple eigenvalue, larger than the real part of any other eigenvalue, with strictly positive left and right eigenvectors. Henceforth, we assume the following.

HYPOTHESIS H1. The matrix \mathbf{K} is irreducible.

The left eigenspace of the 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 a vector $\boldsymbol{\nu}$, which is unique if we choose it having positive entries and verifying $\mathbf{1}^\top \boldsymbol{\nu} = 1$.

To assure the existence and uniqueness of the solution of systems (1)–(3), we assume Hypothesis H2, where we use the notation

$$\mu^*(a) = \sum_{i=1}^N \mu_i(a) \nu_i = \mathbf{1}^\top \mathbf{M}(a) \boldsymbol{\nu}, \quad (4)$$

$$\beta^*(a) = \sum_{i=1}^N \beta_i(a) \nu_i = \mathbf{1}^\top \mathbf{B}(a) \boldsymbol{\nu}. \quad (5)$$

HYPOTHESIS H2.

- (i) $\mu_j, \beta_j \in L^\infty(\mathbf{R}_+)$, $\mu_j(a) \geq 0$, $\beta_j(a) \geq 0$, a.e., $a \in \mathbf{R}_+$, $j = 1, \dots, N$.
- (ii) $\inf_{a \geq 0} \mu^*(a) = \mu_* > 0$.
- (iii) There exists $s_0 \in \mathbf{R}$, $s_0 > -\mu_*$ such that $\int_0^{+\infty} e^{-s_0 a} \beta^*(a) e^{-\int_0^a \mu^*(\sigma) d\sigma} da > 1$ and $\limsup_{a \rightarrow \infty} e^{s_0 a} \|\mathbf{B}(a)\| < +\infty$.

Now, Proposition 3.2 of [9, p. 76] applies. System (1)–(3) has a unique solution for every initial age distribution $\phi \in L^1(\mathbf{R}^+, \mathbf{R}^N)$, and we can associate to it a strongly continuous semigroup of bounded linear operators

$$\begin{aligned} T_\varepsilon(t) : L^1(\mathbf{R}^+, \mathbf{R}^N) &\longrightarrow L^1(\mathbf{R}^+, \mathbf{R}^N), \\ \phi &\longrightarrow T_\varepsilon(t)\phi = \mathbf{n}_\varepsilon(\cdot, t), \end{aligned}$$

where $\mathbf{n}_\varepsilon(\cdot, t)$ is the solution of (1)–(3) corresponding to the initial age distribution ϕ .

Under some additional assumptions, Arino *et al.* [4] show that the semigroup $T_\varepsilon(t)$ exhibits positive asynchronous exponential growth.

3. THE AGGREGATED MODEL

The so-called aggregated system, constructed in detail in [4], is a scalar classical McKendrick model which approximates the dynamics of the total population, henceforth called global variable

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

Mathematically, it reads

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu^*(a)n(a, t), \quad (a > 0, t > 0), \quad (6)$$

$$n(0, t) = \int_0^{+\infty} \beta^*(a)n(a, t) da, \quad (t > 0), \quad (7)$$

$$n(a, 0) = \phi(a), \quad (a > 0). \quad (8)$$

The general theory applies here [9], proving the existence of exponential asynchronous behaviour in the cases where the characteristic equation associated to the problem possesses a unique real simple root which is strictly dominant. In the following, we denote $\{S_0(t)\}_{t \geq 0}$ the semigroup associated to the aggregated model.

4. DECOMPOSITION OF THE SEMIGROUP

In this section, we will establish the main result of this paper: the semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$ associated to the perturbed problem (1)–(3) can be decomposed into a stable part which is precisely $S_0(t)\nu$ and a perturbation of order $O(\varepsilon)$.

With the aim of studying the behaviour of the semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$, we consider the following direct sum decomposition of the space \mathbf{R}^N , whose existence is assured by Hypothesis H1:

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

where $[\nu]$ is the subspace of dimension 1 generated by vector ν and $S = \{\mathbf{v} \in \mathbf{R}^N; \mathbf{1}^\top \mathbf{v} = 0\}$. Observe that \mathbf{K}_S , the restriction of \mathbf{K} to S , is an isomorphism on S with spectrum $\sigma(\mathbf{K}_S) \subset \{\lambda \in \mathbf{C}; \operatorname{Re} \lambda < 0\}$.

We decompose the solutions of system (1)–(3) according to the projections onto the subspaces $[\nu]$ and S . Set

$$\mathbf{n}_\varepsilon(a, t) = p(a, t)\nu + \mathbf{q}(a, t),$$

where we drop the ε under p and q , whenever no confusion is to be expected. The projection onto $[\nu]$ is obtained by left multiplication by $\mathbf{1}$; the complementary projection (onto S) is denoted Π .

Substituting in (1),(2), we obtain the following equations for the components $p(a, t)$ and $q(a, t)$ of $\mathbf{n}_\varepsilon(a, t)$:

$$\frac{\partial p}{\partial a} + \frac{\partial p}{\partial t} = -\mathbf{1}^\top \mathbf{M}(a) \nu p(a, t) - \mathbf{1}^\top \mathbf{M}(a) \mathbf{q}(a, t), \quad (9)$$

$$\frac{\partial \mathbf{q}}{\partial a} + \frac{\partial \mathbf{q}}{\partial t} = -\mathbf{M}_S(a) \nu p(a, t) + \left[\frac{1}{\varepsilon} \mathbf{K}_S - \mathbf{M}_S(a) \right] \mathbf{q}(a, t), \quad (10)$$

$$p(0, t) = \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \nu p(a, t) da + \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \mathbf{q}(a, t) da, \quad (11)$$

$$\mathbf{q}(0, t) = \int_0^{+\infty} \mathbf{B}_S(a) \nu p(a, t) da + \int_0^{+\infty} \mathbf{B}_S(a) \mathbf{q}(a, t) da, \quad (12)$$

where $\mathbf{M}_S(a) = \mathbf{\Pi} \cdot \mathbf{M}(a)$ and $\mathbf{B}_S(a) = \mathbf{\Pi} \cdot \mathbf{B}(a)$ are the projections of $\mathbf{M}(a)$ and $\mathbf{B}(a)$, respectively, onto S .

The general solution of that system can be expressed in terms of the resolvent operators of certain associated problems. From that, we can deduce the dependence of the solution on ε .

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

$$\mathbf{v}'(a) = \left[\frac{1}{\varepsilon} \mathbf{K}_S - \mathbf{M}_S(a) \right] \mathbf{v}(a). \quad (13)$$

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

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

PROOF. See [4, Lemma 1].

From equations (10),(12), we can obtain the function \mathbf{q} in terms of p . Then substituting in (9),(11), we obtain a problem in p . To this end, let us consider the nonhomogeneous problem

$$\frac{\partial \mathbf{q}}{\partial a} + \frac{\partial \mathbf{q}}{\partial t} = \left[\frac{1}{\varepsilon} \mathbf{K}_S - \mathbf{M}_S(a) \right] \mathbf{q}(a, t) + \mathbf{F}(a, t), \quad (14)$$

$$\mathbf{q}(0, t) = \int_0^{+\infty} \mathbf{B}_S(a) \mathbf{q}(a, t) da + \mathbf{G}(t), \quad (15)$$

$$\mathbf{q}(a, 0) = \mathbf{q}_0(a). \quad (16)$$

LEMMA 2. There exists a function $\Phi_\varepsilon = \Phi_\varepsilon(a)$, $a \geq 0$, with values $\in \mathcal{L}(S)$, such that

$$\Phi_\varepsilon'(a) = \left[\frac{1}{\varepsilon} \mathbf{K}_S - \mathbf{M}_S(a) \right] \Phi_\varepsilon(a), \quad a \geq 0,$$

$$\Phi_\varepsilon(0) - \int_0^{+\infty} \mathbf{B}_S(a) \Phi_\varepsilon(a) da = Id.$$

PROOF. We can write

$$\Phi_\varepsilon(a) = R_\varepsilon(a, 0) \Phi_\varepsilon(0),$$

where R_ε is the fundamental matrix in Lemma 1. Then, we obtain for $\Phi_\varepsilon(0)$ the equation

$$\Phi_\varepsilon(0) - \left[\int_0^{+\infty} \mathbf{B}_S(a) R_\varepsilon(a, 0) da \right] \Phi_\varepsilon(0) = Id,$$

which has a solution for ε , small enough, in view of the bound of R_ε in Lemma 1. Let us notice, moreover, that $\lim_{\varepsilon \rightarrow 0^+} \Phi_\varepsilon(0) = Id$. ■

Now, we can perform the change of unknown function

$$\mathbf{q}_1(a, t) = \mathbf{q}(a, t) - \Phi_\varepsilon(a)\mathbf{G}(t),$$

which transforms problem (14)–(16) into a nonhomogeneous problem, with homogeneous condition for $a = 0$

$$\begin{aligned} \frac{\partial \mathbf{q}_1}{\partial a} + \frac{\partial \mathbf{q}_1}{\partial t} &= \left[\frac{1}{\varepsilon} \mathbf{K}_S - \mathbf{M}_S(a) \right] \mathbf{q}_1(a, t) + \mathbf{F}(a, t) - \Phi_\varepsilon(a)\mathbf{G}'(t), \\ \mathbf{q}_1(0, t) &= \int_0^{+\infty} \mathbf{B}_S(a)\mathbf{q}_1(a, t) da, \\ \mathbf{q}_1(a, 0) &= \mathbf{q}_0(a) - \Phi_\varepsilon(a)\mathbf{G}(0). \end{aligned}$$

The solution of this problem can be expressed with the help of the variation-of-constants formula in terms of the semigroup $\{\mathcal{U}_\varepsilon(t)\}_{t \geq 0}$ which gives the solution in $L^1(\mathbf{R}_+, \mathbf{R}^N)$ of the homogeneous problem

$$\frac{\partial \mathbf{q}}{\partial a} + \frac{\partial \mathbf{q}}{\partial t} = \left[\frac{1}{\varepsilon} \mathbf{K}_S(a) - \mathbf{M}_S(a) \right] \mathbf{q}(a, t), \quad (17)$$

$$\mathbf{q}(0, t) = \int_0^{+\infty} \mathbf{B}_S(a)\mathbf{q}(a, t) da, \quad (18)$$

$$\mathbf{q}(a, 0) = \mathbf{q}_0(a) - \Phi_\varepsilon(a)\mathbf{G}(0). \quad (19)$$

To be specific,

$$\mathbf{q}_1(\cdot, t) = \mathcal{U}_\varepsilon(t)[\mathbf{q}_0(\cdot) - \Phi_\varepsilon(\cdot)\mathbf{G}(0)] + \int_0^t \mathcal{U}_\varepsilon(t-\tau)[\mathbf{F}(\cdot, \tau) - \Phi_\varepsilon(\cdot)\mathbf{G}'(\tau)] d\tau.$$

In order to eliminate \mathbf{G}' in the expression for \mathbf{q}_1 , we integrate by parts. Finally, we obtain an expression for \mathbf{q}

$$\mathbf{q}(\cdot, t) = \mathcal{U}_\varepsilon(t)\mathbf{q}_0(\cdot) + \int_0^t \mathcal{U}_\varepsilon(t-\tau)\mathbf{F}(\cdot, \tau) d\tau + \int_0^t \mathcal{V}_\varepsilon(t-\tau)\mathbf{G}(\tau) d\tau, \quad (20)$$

where

$$\mathcal{V}_\varepsilon(t)(a) = \left[\frac{\partial \mathcal{U}_\varepsilon}{\partial t}(t)\Phi_\varepsilon \right](a), \quad (a > 0, t \geq 0). \quad (21)$$

In our case,

$$\begin{aligned} \mathbf{F}(a, t) &= -\mathbf{M}_S(a)\nu p(a, t), \\ \mathbf{G}(t) &= \int_0^{+\infty} \mathbf{B}_S(a)\nu p(a, t) da. \end{aligned}$$

Now, we substitute solution (20) of $\mathbf{q}(\cdot, t)$ into equations (9),(11), obtaining the following system for $p(a, t)$:

$$\begin{aligned} \frac{\partial p}{\partial a} + \frac{\partial p}{\partial t} &= -\mu^*(a)p(a, t) + \mathbf{1}^\top \mathbf{M}(a) \int_0^t \mathcal{U}_\varepsilon(t-\tau)\mathbf{M}_S(a)\nu p(a, \tau) d\tau \\ &\quad - \mathbf{1}^\top \mathbf{M}(a) \int_0^t \mathcal{V}_\varepsilon(t-\tau)(a) \left(\int_0^{+\infty} \mathbf{B}_S(\alpha)\nu p(\alpha, t) d\alpha \right) d\tau \\ &\quad - \mathbf{1}^\top \mathbf{M}(a)\mathcal{U}_\varepsilon(t)\mathbf{q}_0(a), \\ p(0, t) &= \int_0^{+\infty} \beta^*(a)p(a, t) da - \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \left(\int_0^t \mathcal{U}_\varepsilon(t-\tau)\mathbf{M}_S(a)\nu p(a, \tau) d\tau \right) da \\ &\quad + \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \left(\int_0^t \mathcal{V}_\varepsilon(t-\tau)(a) \left(\int_0^{+\infty} \mathbf{B}_S(\alpha)\nu p(\alpha, \tau) d\alpha \right) d\tau \right) da \\ &\quad + \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) (\mathcal{U}_\varepsilon(t)\mathbf{q}_0)(a) da. \end{aligned}$$

With the aim of simplifying the notations, we define, for each $t > 0$ fixed, the following two operators:

$$\begin{aligned}\mathcal{D}_\varepsilon(t) &: C([0, t], L^1(\mathbf{R}_+)) \longrightarrow L^1(\mathbf{R}_+), \\ \mathcal{B}_\varepsilon(t) &: C([0, t], L^1(\mathbf{R}_+)) \longrightarrow \mathbf{R},\end{aligned}$$

$$\begin{aligned}\mathcal{D}_\varepsilon(t)p(a) &= \mathbf{1}^\top \mathbf{M}(a) \int_0^t \mathcal{U}_\varepsilon(t-\tau) \mathbf{M}_S(a) \nu p(a, \tau) d\tau \\ &\quad - \mathbf{1}^\top \mathbf{M}(a) \int_0^t \mathcal{V}_\varepsilon(t-\tau)(a) \left(\int_0^{+\infty} \mathbf{B}_S(\alpha) \nu p(\alpha, t) d\alpha \right) d\tau,\end{aligned}\tag{22}$$

$$\begin{aligned}\mathcal{B}_\varepsilon(t)p &= - \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \left(\int_0^t \mathcal{U}_\varepsilon(t-\tau) \mathbf{M}_S(a) \nu p(a, \tau) d\tau \right) da \\ &\quad + \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) \left(\int_0^t \mathcal{V}_\varepsilon(t-\tau)(a) \left(\int_0^{+\infty} \mathbf{B}_S(\alpha) \nu p(\alpha, \tau) d\alpha \right) d\tau \right) da.\end{aligned}\tag{23}$$

Let us denote

$$f_\varepsilon(a, t) = -\mathbf{1}^\top \mathbf{M}(a) (\mathcal{U}_\varepsilon(t) \mathbf{q}_0)(a),\tag{24}$$

$$g_\varepsilon(t) = \int_0^{+\infty} \mathbf{1}^\top \mathbf{B}(a) (\mathcal{U}_\varepsilon(t) \mathbf{q}_0)(a) da.\tag{25}$$

Finally, we can write the system verified by $p(a, t)$ in the form

$$\frac{\partial p}{\partial a} + \frac{\partial p}{\partial t} = -\mu^*(a)p(a, t) + (\mathcal{D}_\varepsilon(t)p)(a) + f_\varepsilon(a, t), \quad (a > 0, t > 0),\tag{26}$$

$$p(0, t) = \int_0^{+\infty} \beta^*(a)p(a, t) da + \mathcal{B}_\varepsilon(t)p + g_\varepsilon(t), \quad (t > 0),\tag{27}$$

$$p(a, 0) = p_0(a), \quad (a > 0).\tag{28}$$

Integrating system (26)–(28) along the characteristic lines of the operator $(\frac{\partial}{\partial a}) + (\frac{\partial}{\partial t})$, we can formulate the problem in terms of proving existence of a fixed point for an operator.

Lemma 1 and straightforward calculations yield the bounds established in the following lemma.

LEMMA 3.

- (a) The semigroup $\{\mathcal{U}_\varepsilon(t)\}_{t \geq 0}$ satisfies the following estimate, for some positive constants k_4, k_5 , and the constant k_1 given in Lemma 1:

$$\|\mathcal{U}_\varepsilon(t)\| \leq k_5 e^{(k_4 - k_1/\varepsilon)t}, \quad (t \geq 0).$$

- (b) The function $\mathcal{V}_\varepsilon(t)(\cdot) : \mathbf{R}_+ \longrightarrow \mathcal{L}(\mathbf{R}^N)$, defined in (21), satisfies the following estimate, for some positive constants k_6, k_7 :

$$\|\mathcal{V}_\varepsilon(t)\|_{L^1} \leq k_7 e^{(k_6 - k_1/\varepsilon)t}, \quad (t \geq 0).$$

- (c) The operators $\mathcal{D}_\varepsilon(t), \mathcal{B}_\varepsilon(t)$ defined in (22), (23) satisfy the following estimates for some positive constants k_8, k_9 :

$$\begin{aligned}\|\mathcal{D}_\varepsilon(t)p\|_{L^1(\mathbf{R}_+)} &\leq \varepsilon k_8 \left[e^{(k_2 - k_1/\varepsilon)t} - 1 \right] \sup_{\tau \in [0, t]} \|p(\cdot, \tau)\|_{L^1}, \\ |\mathcal{B}_\varepsilon(t)p| &\leq \varepsilon k_9 \left[e^{(k_2 - k_1/\varepsilon)t} - 1 \right] \sup_{\tau \in [0, t]} \|p(\cdot, \tau)\|_{L^1}, \quad (t \geq 0).\end{aligned}$$

Denote by $\rho_0(a, \alpha)$ the resolvent function of the problem

$$\frac{dz}{da} = -\mu^*(a)z(a), \quad \rho_0(\alpha, \alpha) = 1.$$

Observe that $\rho_0(a, 0) = e^{-\int_0^a \mu^*(s) ds}$ is the resolvent associated to the aggregated problem (6)–(8). After standard calculations, we obtain the following equations.

(i) For $a > t$,

$$\begin{aligned} p(a, t) &= \rho_0(a, a-t)p_0(a-t) \\ &+ \int_0^t \rho_0(a, a-t+\sigma)[(\mathcal{D}_\varepsilon(\sigma)p)(a-t+\sigma) + f_\varepsilon(a-t+\sigma, \sigma)] d\sigma. \end{aligned} \quad (29)$$

(ii) For $a < t$,

$$\begin{aligned} p(a, t) &= \rho_0(a, 0) \left[\int_0^{+\infty} \beta^*(\alpha)p(\alpha, t-a) d\alpha + \mathcal{B}_\varepsilon(t-a)p + g_\varepsilon(t-a) \right] \\ &+ \int_0^a \rho_0(a, \sigma)[(\mathcal{D}_\varepsilon(t-a+\sigma)p)(\sigma) + f_\varepsilon(\sigma, t-a+\sigma)] d\sigma. \end{aligned} \quad (30)$$

Both equations (29) and (30) can be collected in a single equation of the form

$$p = \mathcal{F}(\varepsilon, p), \quad (31)$$

where the operator $\mathcal{F}(\varepsilon, p)$ can be decomposed into the sum of three terms.

(j) A term \mathcal{H}_0 , independent of ε ,

$$\mathcal{H}_0(p)(a, t) = \begin{cases} 0, & (a > t), \\ \rho_0(a, 0) + \int_0^{+\infty} \beta^*(\alpha)p(\alpha, t-a) d\alpha, & (t > a). \end{cases}$$

(jj) A term $\mathcal{A}(\varepsilon, p)$, dependent on ε and linear in p ,

$$\mathcal{A}(\varepsilon, p)(a, t) = \begin{cases} \int_0^t \rho_0(a, a-t+\sigma)(\mathcal{D}_\varepsilon(\sigma)p)(a-t+\sigma) d\sigma, & a > t, \\ \int_0^a \rho_0(a, \sigma)(\mathcal{D}_\varepsilon(t-a+\sigma)p)(\sigma) d\sigma + \rho_0(a, 0)\mathcal{B}_\varepsilon(t-a)p, & t > a. \end{cases}$$

(jjj) A nonhomogeneous term $\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)(a, t)$, only dependent on the initial conditions

$$\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)(a, t) = \begin{cases} \rho_0(a, a-t)p_0(a-t) + \int_0^t \rho_0(a, a-t+\sigma)f_\varepsilon(a-t+\sigma, \sigma) d\sigma, & (a > t), \\ \rho_0(a, 0)g_\varepsilon(t-a) + \int_0^a \rho_0(a, \sigma)f_\varepsilon(\sigma, t-a+\sigma) d\sigma, & (t > a). \end{cases}$$

Therefore, we have

$$\mathcal{F}(\varepsilon, p) = \mathcal{H}_0(p) + \mathcal{A}(\varepsilon, p) + \mathcal{J}(\varepsilon, p_0, \mathbf{q}_0).$$

It is possible to choose an exponential norm in $C = C([0, T]; L^1(\mathbf{R}_+))$ ($T > 0$), such that the operator $\mathcal{H}_0 + \mathcal{A}(\varepsilon, \cdot)$ is a strict contraction in C for every $\varepsilon \leq \varepsilon_0$. We can write the solution p of equation (31) in the form

$$p = (Id - \mathcal{H}_0 - \mathcal{A}(\varepsilon, \cdot))^{-1}[\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)]. \quad (32)$$

Let us define

$$\mathcal{J}(0, p_0, \mathbf{0})(a, t) = \begin{cases} \rho_0(a, a-t)p_0(a-t), & (a > t), \\ 0, & (a < t). \end{cases}$$

We can then write the following asymptotic expression for the solution p of equation (32):

$$p = [Id - \mathcal{H}_0]^{-1}(\mathcal{J}(0, p_0, \mathbf{0})) + \varepsilon B(\varepsilon, p_0, \mathbf{q}_0), \quad (33)$$

where B is an operator such that, for some constant $C_1 > 0$,

$$\|B(\varepsilon, p_0, \mathbf{q}_0)(\cdot, t)\|_{L^1(\mathbf{R}_+)} \leq C_1 e^{-\mu_* t} \|(p_0, \mathbf{q}_0)\|_{L^1(\mathbf{R}_+)}. \quad (34)$$

The term $(Id - \mathcal{H}_0)^{-1}[\mathcal{J}(0, p_0, \mathbf{0})]$ is the solution of equations (26) and (27) for $\varepsilon = 0$, which is just the aggregated model (6),(7) with initial age distribution $p_0(a)$. Then, it can be expressed in terms of the semigroup $\{S_0(t)\}_{t \geq 0}$, as $S_0(t)p_0$.

The main result of this paper is stated in terms of the perturbed semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$ in the following theorem.

THEOREM 1. *For every $\varepsilon > 0$, small enough, and some constant $C_2 > 0$, it is verified that*

$$(T_\varepsilon(t)\phi)(a) = (S_0(t)p_0)(a)\nu + \mathcal{U}_\varepsilon(t)\mathbf{q}_0(a) + \varepsilon B(\varepsilon, p_0, \mathbf{q}_0)(a, t) + O\left(\varepsilon e^{(C_2 - k_1/\varepsilon)t}\right), \quad (35)$$

where $\{S_0(t)\}_{t \geq 0}$ is the semigroup associated to the aggregated model (6)–(8) and $\phi = p_0\nu + \mathbf{q}_0$, with $\mathbf{q}_0 \in S$, is the initial age distribution.

COROLLARY 1. *For each $t > 0$, we have*

$$\lim_{\varepsilon \rightarrow 0} T_\varepsilon(t)\phi = S_0(t)p_0\nu,$$

where the limit is taken in $L^1(\mathbf{R}_+, \mathbf{R}^N)$.

From Lemma 3, we can obtain the convergence in t and ε

$$\lim_{\varepsilon \rightarrow 0, (t/\varepsilon) \rightarrow \infty} [T_\varepsilon(t)\phi - S_0(t)p_0\nu] = 0.$$

Therefore, the convergence is uniform if $t \in [b, +\infty[$ for each $b > 0$, but is not uniform in $[0, +\infty[$. In fact, for $t = 0$ and each initial age distribution ϕ , we have

$$\lim_{\varepsilon \rightarrow 0} T_\varepsilon(0)\phi = \phi,$$

whereas if the limit (35) were uniform,

$$\lim_{\varepsilon \rightarrow 0} T_\varepsilon(0)\phi = p_0\nu,$$

which yields a contradiction if $\phi \notin [\nu]$.

5. CONCLUSION

Let us interpret formula (35). The components of ν are positive and sum up to one, and they represent a distribution of individuals in the patches. $(S_0(t)p_0)(a)$ gives the total number of individuals of age a . Conditions stated in [4] ensure that the semigroup $S_0(t)$ has a positive asynchronous exponential growth. For each $t > 0$, the above formula yields that $T_\varepsilon(t)\phi \rightarrow (S_0(t)p_0)\nu$, in L^1 , as $\varepsilon \rightarrow 0$. But the convergence is not uniform in t . For $\varepsilon = 0$, that is to say, if we assume that the transition time between any two patches is zero (or say, infinitely small), the equation reduces to $\mathbf{Kn}(a, t) = 0$, with the same boundary condition at $a = 0$. In this case, the

population moves in such a way that it instantly occupies the patches according to the desired distribution. In practice, some time is needed for individuals to jump between two patches, and formula (35) tells us how long it takes for any given distribution to reach a neighborhood of the desired distribution. It yields the following: for every $0 < \eta < (k_1/k_4)$ (k_1 and k_4 given in the bound of Lemma 3a), there exists $\kappa > 0$ such that for every $0 < \varepsilon < \eta/(C + 1)$ (C given in bound (34)) and $t \geq \kappa\varepsilon$, and every initial value ϕ , we have $\|T_\varepsilon(t)\phi - S_0(t)p_0\nu\| \leq \eta\|\phi\|$. The solution $S_0(t)p_0\nu$ is typically the outer solution in the singular perturbation theory, while $S_0(t)p_0$ is the solution of the aggregated system in the sense of aggregation theory; $a = 0$ plays the role of the boundary layer associated with a singular perturbation, and the above estimate of the region of nonuniform convergence indicates that the boundary layer has a thickness of the order of ε .

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 approximation lacks the possibility of measuring the time spent in the transitory state as mentioned in the above paragraph. 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.

REFERENCES

1. C. Koutsikopoulos, L. Fortier and J.A. Gagne, Cross-shelf dispersion of Dover sole (*Solea solea*) eggs and larvae in Biscay Bay and recruitment to inshore nurseries, *Jour. Plankton Res.* **13**, 923–945 (1991).
2. G. Champalbert and C. Koutsikopoulos, Behaviour, transport and recruitment of Biscay Bay sole (*Solea solea*): Laboratory and field studies, *J. Mar. Biol. Ass. U.K.* **75**, 93–108 (1995).
3. O. Arino, C. Koutsikopoulos and A. Ramzi, Elements of a model of the evolution of the density of a sole population, *J. Biol. Systems* **4**, 445–458 (1996).
4. O. Arino, E. Sánchez and R. Bravo de la Parra, A model of an age-structured population in a multipatch environment, *Mathl. Comput. Modelling* **27** (4), 137–150 (1998).
5. R. Bravo de la Parra, P. Auger and E. Sánchez, Aggregation methods in discrete models, *J. Biol. Systems* **3**, 603–612 (1995).
6. E. Sánchez, R. Bravo de la Parra and P. Auger, Linear discrete models with different time scales, *Acta Biotheoretica* **43**, 465–479 (1995).
7. J.A.J. Metz and O. Diekmann, *The Dynamics of Physiologically Structured Populations*, LNB 68 Springer-Verlag, Berlin, (1986).
8. E. Seneta, *Nonnegative Matrices and Markov Chains*, Springer-Verlag, (1981).
9. G.F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics*, Marcel Dekker, New York, (1985).