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A SINGULAR PERTURBATION IN AN AGE-STRUCTURED POPULATION MODEL*

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Abstract. The aim of this work is to study a model of age-structured population with two time scales: the first one is slow and corresponds to the demographic process and the second one is comparatively fast and describes the migration process between different spatial patches. 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. The main results of the work are that, for $\varepsilon > 0$ small enough, the solutions of the system can be approximated by means of the solutions of a scalar problem, where the fast process has been avoided by supposing it has attained an equilibrium. The state variable of the scalar system represents the global density of the population. The birth equation causes a singularity for ages close to 0 to appear, which produces a boundary layer type phenomenon.

This work originated from the study of some fisheries of the West Coast of the Atlantic Ocean, namely, small pelagic fish (anchovy and sardine) and flatfish (sole) of the Bay of Biscay. The general model of fish population dynamics considered throughout the paper was elaborated as part of this study.

Key words. structured population dynamics, singular perturbations, approximate aggregation of variables, two time scales

AMS subject classifications. 92D25, 35B25

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1. Introduction.

Nature offers many examples of systems where several events occur at different time scales. It is then common practice to consider those events occurring at the fastest scale as being instantaneous with respect to the slower ones, which results in a lesser number of variables or parameters needed to describe the evolution of the system. A subsequent issue is to determine how far the results obtained from the reduced system are from the real ones. Several mathematical methods have been developed in relation with the two above-mentioned issues, that is, reduction and an estimation of the discrepancy between the complete system and the systems arising from the reduction; the best known are averaging methods, singular perturbation methods, and aggregation methods. Regarding applications of these methods, by far the most important ones have been in physics, chemistry, mechanics, and industrial processes, and concern essentially averaging and singular perturbation

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methods (see, for example, the latest edition of the book by Kevorkian and Cole [15]; see also the special issue of the *SIAM Journal on Applied Mathematics* devoted to singular perturbation theory [30]). Life sciences are more concerned with aggregation methods. This is probably due to the way scales differences occur in life sciences: we see, in various contexts, interactions of the large and the small (whales eating krill, blood cells flowing in our veins, bacteria transforming our food, etc.) which lead us to disregard any structure in the small or fast species compared to the large or slow ones. Aggregation was, and still is, first of all an implicit common practice. The possible importance of aggregation in biological and ecological phenomena was recognized only recently. The development of aggregation methods has been notably undertaken within the past 10 years by Auger [6], in the frame of ordinary differential equations. The main effort was spent in deriving so-called aggregated systems and a general formal computational method, the quick derivation method, was described by Auger in a large class of systems possessing one or several invariants. The method was refined and a number of examples were investigated by Auger and his collaborators [7, 8, 9]. Recently, aggregation methods were developed in the context of discrete dynamical systems by Auger, Bravo de la Parra, and Sanchez [10, 11, 12, 28]. Both a quick derivation method and error estimates were obtained, and a few examples were worked out.

In this paper, a general linear model with both a continuous age structure and a finite spatial structure is considered. It is assumed that discrete migration processes take place between spatial patches at a frequency much higher than the demographic events—so high that one nearly cannot see them. The impression is that of a spatially homogeneous age-dependent population governed by a von Foerster equation with birth and death coefficients averaged from the original patch-dependent coefficients through a weighted average. The weights are computed in terms of the migration matrix and are in fact the mark of the *hidden* underlying spatial structure.

Spatial homogeneity is reached after a short time: the time it takes newborns to adapt their migrations between the patches in such a way as to maintain the weight of each patch. This time length corresponds to the thickness of a boundary layer near age $a = 0$.

The model covers a variety of situations in the modeling of fish population dynamics, namely, the segment of the fish life cycle where fish undergo movements in the water column, from below the surface down to the seabed or the top of a lower sea layer, according to an essentially circadian rhythm. This work was in fact motivated by the study of two species which are subject to industrial fishing by both French and Spanish fleets of the Atlantic Ocean: *Solea solea*, the common sole of the Bay of Biscay [13], [17], [4], and *Engraulis encrasicholus*, the anchovy of the Bay of Biscay [33], [5]. The anchovy is a pelagic fish throughout its life, that is, it lives in the water column, while the sole is pelagic in the larval stage and becomes benthic after its metamorphosis into a flatfish [32].

In [4], the authors modeled the migration of the sole from its spawning grounds (60 to 80 miles from the coast) to the nursery grounds (in bays or river estuaries less than 20 miles from the coast) essentially as a horizontal diffusion process taking place during the larval stage. In the model presented in [4], the effect of vertical migration on the horizontal movement was averaged throughout the whole water column to produce a supposedly constant shoreward velocity. What we present here is both a general and a rigorous treatment of averaging in the framework adopted in [4] in which vertical motion was considered a fast process compared to the process of nearing the coast.

In order to keep our readership large enough and at the same time maintain a satisfactory level of generality, spatial dependence has been restricted to the vertical. This means that after averaging has been performed, using the aggregation method, the model at hand is age-only dependent. Another simplifying assumption of our model is that it does not discriminate among the stages. Such a discrimination is usually done via growth equations [4], [2] and is not taken into account here. Research toward allowing horizontal spatial dependence, together with vertical dependence and incorporating growth equations into the model is in progress.

The framework chosen in this paper is deliberately linear in order to focus readers' attention on the main mechanism. In future work, we plan to relax this strong assumption.

The organization of the paper is as follows. Section 2 presents the general model to be considered throughout and the main aggregation result. The situation of fish population dynamics is explained in detail in subsection 2.3, mainly in the context of *Engraulis encrasicholus*. Section 3 deals with the solution operator of the perturbed problem and gives an asymptotic formula (Theorem 3.8). Section 4 deals with the important issue of age-asynchronous distribution and shows that, under some conditions, asynchronous distribution of the aggregated system is the limit of the same property for the full (nonaggregated) system. Section 5 concludes the paper by discussing the way the nonaggregated solution operator approaches the aggregated one and by illustrating some of the results on the fish dynamics example.

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.

Let $n_i(a,t)$ be the population density in patch i ($i = 1, \ldots, N$) 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, and

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

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

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

Let $k_{ij}(a)$ be the age-specific migration rate from patch j to patch i, $i \neq j$, and

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

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

The model based upon the classical McKendrick–von Foerster model for an age-structured population is as follows:

Balance law:

$$\frac{\partial \mathbf{n}}{\partial a} + \frac{\partial \mathbf{n}}{\partial t} = [-\mathbf{M}(a) + R\,\mathbf{K}(a)]\,\mathbf{n}(a,t) \qquad (a > 0, t > 0). \tag{2.1}$$

Birth law:

$$\mathbf{n}(0,t) = \int_0^{+\infty} \mathbf{B}(a)\mathbf{n}(a,t)da \qquad (t > 0). \tag{2.2}$$

Initial age distribution:

$$\mathbf{n}(a,0) = \boldsymbol{\phi}(a) \qquad (t > 0), \tag{2.3}$$

where $R > 0$ is a large constant.

Matrix $\mathbf{K}(a)$ has nonnegative off-diagonal elements and the sum of its columns is equal to zero. If we also assume that $\mathbf{K}(a)$ is irreducible, then Theorem 2.6 of [29, pp. 46–47] applies and we have, for every $a > 0$, 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* $\mathbf{K}(a)$ *is irreducible for every* $a > 0$*.*

The left eigenspace of matrix $\mathbf{K}(a)$ associated with the eigenvalue 0 is generated by vector $\mathbf{1} = (1, \dots, 1)^{\mathsf{T}} \in \mathbf{R}^N$. The right eigenspace is generated by vector $\boldsymbol{\nu}(a)$ and is unique if we choose it having positive entries and verifying $\mathbf{1}^{\mathsf{T}}\,\boldsymbol{\nu}(a) = 1$.

We assume $\mathbf{K}(\cdot)$ is of class C^1 and $\boldsymbol{\nu}(\cdot)$, $\boldsymbol{\nu}'(\cdot)$ are bounded; that is, there exist two positive constants M_1, M_2, such that for all $a \geq 0$, $\|\boldsymbol{\nu}(a)\| \leq M_1$, $\|\boldsymbol{\nu}'(a)\| \leq M_2$.

We use the notation

$$\mu^*(a) = \sum_{i=1}^{N} \mu_i(a)\nu_i(a) = \mathbf{1}^{\mathsf{T}}\mathbf{M}(a)\boldsymbol{\nu}(a), \tag{2.4}$$

$$\beta^*(a) = \sum_{i=1}^{N} \beta_i(a)\nu_i(a) = \mathbf{1}^{\mathsf{T}}\mathbf{B}(a)\boldsymbol{\nu}(a). \tag{2.5}$$

The mortality and birth rates satisfy the following conditions.

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* $\limsup_{a\to\infty} e^{s_0 a}\|\mathbf{B}(a)\| < +\infty$.

We transform the initial system (2.1)–(2.3) by defining $\varepsilon = 1/R$ and writing (2.1) in the singular perturbed form

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

For every initial age distribution $\boldsymbol{\phi} \in L^1(\mathbf{R}_+, \mathbf{R}^N)$, the problem (2.1)–(2.3) has a unique solution and therefore we can associate with it a strongly continuous semigroup of linear operators

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

where $\mathbf{n}_\varepsilon(\cdot, t)$ is the solution of (2.1)–(2.3) corresponding to the initial condition $\boldsymbol{\phi}$.

The infinitesimal generator of the semigroup is

$$A_\varepsilon\boldsymbol{\phi} = -\boldsymbol{\phi}' + \left[-\mathbf{M}(a) + \frac{1}{\varepsilon}\mathbf{K}(a)\right]\boldsymbol{\phi} \tag{2.6}$$

with domain

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

(see [35]).

2.1. The aggregated model. We build up a model which describes the dynamics of the total population:

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

The exact model satisfied by the new variable $n(a,t)$, henceforth called the global variable, is obtained by adding up the variables $n_i(a,t)$ in system (2.1)–(2.3):

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\sum_{i=1}^{N} \mu_i(a) n_i(a,t) \qquad (a > 0,\, t > 0), \tag{2.7}$$

$$n(0,t) = \int_0^{+\infty} \left(\sum_{i=1}^{N} \beta_i(a) n_i(a,t) \right) da \qquad (t > 0), \tag{2.8}$$

$$n(a,0) = \phi(a) = \sum_{i=1}^{N} \phi_i(a) \qquad (a > 0). \tag{2.9}$$

In order to obtain a system with the global variable as the unique state variable we propose the following approximation:

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

which implies that

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

and

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

The approximated model for the density of the total population, which we call the aggregated system, is the following:

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu^*(a) n(a,t) \qquad (a > 0, t > 0), \tag{2.10}$$

$$n(0,t) = \int_0^{+\infty} \beta^*(a) n(a,t) da \qquad (t > 0), \tag{2.11}$$

$$n(a,0) = \phi(a) \qquad (a > 0). \tag{2.12}$$

2.2. Asymptotic behavior of the aggregated model. The aggregated system is a classical linear model, called a Sharpe–Lotka–McKendrick model in [35]. The general theory applies here, yielding exponential asynchronous behavior in the case where the characteristic equation associated with the problem possesses a unique real simple root which is strictly dominant.

From Hypothesis H2 (i) and (ii) we have that the function

$$F(\lambda) = \int_0^{+\infty} e^{-\lambda a}\beta^*(a)e^{-\int_0^a \mu^*(\sigma)d\sigma}da$$

is defined for $\mathrm{Re}\lambda > -\mu_*$. $F(\lambda)$ is continuous, strictly decreasing for real values of λ, and $\lim_{\lambda\to\infty} F(\lambda) = 0$. Since $F(s_0) > 1$, from Hypothesis H2 (iii), we conclude that the characteristic equation

$$1 = \int_0^{+\infty} e^{-\lambda a}\beta^*(a)e^{-\int_0^a \mu^*(\sigma)d\sigma}da \tag{2.13}$$

has a unique real root $\lambda_0 > s_0$.

The fact that $\mu_* > 0$ implies that if $F(0) > 1$, then $\lambda_0 > 0$; if $F(0) = 1$, then $\lambda_0 = 0$; and if $F(0) < 1$, then $\lambda_0 < 0$.

Now Theorem 4.9 of [35, p. 187] applies.

PROPOSITION 2.1. *Let* $\lambda_0 \in \mathbf{R}$ *be the real solution of the characteristic equation* (2.13). *Then*

$$\lim_{t\to\infty} e^{-\lambda_0 t}n(a,t) = e^{-\lambda_0 a}e^{-\int_0^a \mu^*(\sigma)d\sigma}c(\phi),$$

where $n(a,t)$ *is the unique solution of the aggregated model* (2.10)–(2.12) *corresponding to the initial age distribution* $\phi \in L^1(\mathbf{R}_+)$ *and* $c(\phi) > 0$ *is a constant that depends on* ϕ. *The limit is taken in* $L^1(\mathbf{R}_+)$.

This proposition establishes that the semigroup $\{S_0(t)\}_{t\geq 0}$ associated with the solutions of the aggregated model (2.10)–(2.12) has the asynchronous exponential growth property with associated malthusian parameter λ_0 and asymptotic distribution $\theta_0(a) = e^{-\lambda_0 a}e^{-\int_0^a \mu^*(\sigma)\,d\sigma}$.

2.3. An application to fish dynamics. This work was motivated by the study of fish dynamics and the role played by the position of fish in the water column and diel migration inside the column. For several fish species, including *Engraulis encrasicholus* [19], an anchovy present in the Bay of Biscay, or the pelagic stage of *Solea solea*, the common sole of the same area [4], many concordant field data indicate the following features [22], [21]: (1) a distribution of the species throughout the water column with one or several peaks; (2) this distribution changes during the life of individuals (ontogenetic migration) with the range increasing through time; (3) distribution also changes during the day, with most of the population being near the surface at night and closer to the lower part of the water column during daylight.

Vertical displacements are the result of a number of factors: sea turbulence, reaction to light, quest for food, and energy cost minimization (a possible explanation for night migration toward the surface, which is generally warmer than the deeper layers of the sea and thus, in particular, more suited for digestion). An evolutionary advantage of migration toward the lower layer of the sea during the day could be that it gives better protection to small fish from predation by large fish.

At the level of a life stage, such as the larval stage or the juvenile stage (for the anchovy), or the much longer adult stage (for the anchovy), vertical migration may be considered a rather fast process, occurring many times during a single stage, especially after the swim bladder has become functional (about 10 days or more after egg fertilization in the case of the anchovy (see [22, Fig. 4.9])). The day (24 hours) is the fast time scale, compared to the time spanned from fertilization to the juvenile stage.

It is tempting, when describing the demographic processes of those fish, to forget the details about vertical migration. This means working with the population aggregated over the whole column. However, a question immediately arises: Can heterogeneity entailed by differences in birth rates and death rates along the water column and the vertical movement can be aggregated? This is precisely the issue dealt with in this paper and it will be shown that, under quite standard hypotheses, the aggregated equations obtained by the procedure explained in section 2 approximate the full system to the order of some number $\varepsilon > 0$, where ε represents the rate of the fast time scale to the slow scale.

We return to the fish problem. From field studies, one can determine a migration matrix, a function of age and time [26], [17], [21]. For simplicity, we omit time dependence here. In the absence of data on the migration between layers, we treat the migration as a random process activated at each small time interval, the probability for an individual to go from patch i to patch j being the same for all $i \neq j$ and equal to the average proportion of individuals of age a occupying patch j during this time interval. So, this yields

$$k_{ij}(a) = p_i(a), \text{ if } j \neq i; \quad k_{ii}(a) = p_i(a) - 1.$$

Assuming that each $p_i > 0$ immediately yields that the matrix $\mathbf{K}$ is irreducible, that is, Hypothesis H1 holds. From a straightforward computation, we get that $\nu_i(a) = p_i(a)$.

The migration modeled here is of a very different nature, dependent on the stage that the fish is in: while for adults it is essentially governed by a circadian cycle and the quest of food, in the early larval stage of anchovy (before the swim bladder becomes functional [22] it is mainly governed by physical turbulence [31], [24] to which the animal responds with more or less intensity depending upon its size [22].

Let us now look at the two main components of a demographic model: mortality and reproduction. Mortality is probably dependent on depth, especially in the larval stage of fish. Depth acts through the temperature which generally decreases down the water column: a lower temperature means a slower development and thus a higher mortality within a given stage (see [25] and [22, Fig. 4.20]). Mortality is also dependent on age; for the anchovy, the structure of the mortality function is strongly related to its stage: it is high during the egg stage, due to both biological defects and predation on egg aggregates; it decreases steadily during the larval stage, where it is essentially due to starvation [14], [34]; mortality at the juvenile and adult stages is impacted by harvest by humans, much more for the adult fish which are subject to industrial fishing more than the juveniles which serve as bait for other harvested species [33].

As for the birth rate $\beta(a)$, it depends both on depth and age: for the anchovy, reproduction takes place at night (between 10 pm and 2 am, with a peak around midnight) and is, with few exceptions, done below the surface in the few first layers. Aggregation of the spawned eggs may be determined using the migration matrix associated with night migrations. Instead of modeling the birth as a function of the population, it is sometimes possible to use field data. For the anchovy of the Bay of Biscay, egg samples are collected throughout the whole spawning area, and egg production is estimated using the DEPM (daily egg production method) [18], [20]. Although it is possible to arrange for the samplings to discriminate along the depth, this is both costly and time-consuming: a preferred technique consists of collecting the material contained in a straight cylinder of water going from the surface to the seabed, thus providing the egg data for the aggregated model ([18]; see also [32]).

Let us now see how the above information can be combined into a model. A preliminary step is the selection, for each of the processes, of the appropriate time scale: the demographic time unit is the mean duration of a group of egg and/or larval substages, say, of the order of 10 to 20 days. Mortality in a given group is evaluated as the ratio of the number of individuals of that group not reaching the next group to the number of individuals of the group. During the same time unit, migration has been activated 10 or more times so that the migration time unit is a tenth or less of the demographic time unit. More generally, we denote by ε the fraction of the demographic time unit corresponding to the duration of a single migratory activation, that is to say, the demographic time unit. From this, it follows that the matrix $\mathbf{K}(a)$ has to be multiplied by $R = 1/\varepsilon$ (according to the notation used in (2.1)) when writing the equation for the variation of the population.

Finally, an estimate of the initial population (that is, the population present at a given fixed time) can be deduced from surveys of fishing captures and an estimate of the fishing effort. Such estimates discriminate among age and the geographic area where fish have been captured but will usually consider fish summed up throughout the whole water column. Thus, they are well suited to the aggregated model, while they are not especially adapted to an age- and space-structured model.

3. The semigroup associated with the perturbed problem. In this section we will obtain the main result of this paper: The semigroup $\{T_\varepsilon(t)\}_{t\geq 0}$ associated with the perturbed problem (2.1)–(2.3) can be decomposed into a stable part which is precisely $S_0(t)\boldsymbol{\nu}(\cdot)$ and a perturbation of order $O(\varepsilon)$.

With the aim of studying the behavior 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 ensured by Hypothesis H1:

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

where $[\boldsymbol{\nu}(a)]$ is the subspace of dimension 1 generated by the vector $\boldsymbol{\nu}(a)$ and $S = \{\mathbf{v} \in \mathbf{R}^N \ ; \ \mathbf{1}^T\mathbf{v} = 0\}$. We notice that S is the same for all a, because it is orthogonal to vector $\mathbf{1}$, and moreover $\mathbf{K}_S(a)$, the restriction of $\mathbf{K}(a)$ to S, is an isomorphism on S with spectrum $\sigma(\mathbf{K}_S(a)) \subset \{\lambda \in \mathbf{C} \ ; \ \operatorname{Re}\lambda < 0\}$.

We decompose the solutions of (2.1)–(2.3) according to the projections onto the subspaces $[\boldsymbol{\nu}(a)]$ and S, that is to say,

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

The projection onto $[\boldsymbol{\nu}(a)]$ is obtained by premultiplying by $\mathbf{1}$. We denote by $\Pi(a)$ the complementary projection onto S. As $\mathbf{1}^T\boldsymbol{\nu}(a) = 1$, we have $\mathbf{1}^T\boldsymbol{\nu}\,'(a) = 0$, which means that $\boldsymbol{\nu}'(a) \in S$, for every a.

Substituting in (2.1), (2.2) we obtain the following equations for the components $p_\varepsilon(a,t)$ and $\mathbf{q}_\varepsilon(a,t)$ of $\mathbf{n}_\varepsilon(a,t)$:

$$\frac{\partial p_\varepsilon}{\partial a} + \frac{\partial p_\varepsilon}{\partial t} = -\mathbf{1}^\mathsf{T}\mathbf{M}(a)\boldsymbol{\nu}(a)p_\varepsilon(a,t) - \mathbf{1}^\mathsf{T}\mathbf{M}(a)\mathbf{q}_\varepsilon(a,t), \tag{3.1}$$

$$\frac{\partial \mathbf{q}_\varepsilon}{\partial a} + \frac{\partial \mathbf{q}_\varepsilon}{\partial t} = -\left[\mathbf{M}_S(a)\boldsymbol{\nu}(a) + \boldsymbol{\nu}'(a)\right]p_\varepsilon(a,t) + \left[\frac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a)\right]\mathbf{q}_\varepsilon(a,t), \tag{3.2}$$

$$p_\varepsilon(0,t) = \int_0^{+\infty} \mathbf{1}^\mathsf{T}\mathbf{B}(a)\boldsymbol{\nu}(a)p_\varepsilon(a,t)da + \int_0^{+\infty} \mathbf{1}^\mathsf{T}\mathbf{B}(a)\mathbf{q}_\varepsilon(a,t)da, \tag{3.3}$$

$$\mathbf{q}_\varepsilon(0,t) = \int_0^{+\infty} \mathbf{B}_S(a)\boldsymbol{\nu}(a)p_\varepsilon(a,t)da + \int_0^{+\infty} \mathbf{B}_S(a)\mathbf{q}_\varepsilon(a,t)da, \tag{3.4}$$

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

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.

Hypothesis H3. Let $R_\varepsilon(a,\alpha)$, $(a \geq \alpha)$, with $R_\varepsilon(\alpha,\alpha) = I$, be the fundamental matrix of the homogeneous differential system

$$\mathbf{v}'(a) = \left[\frac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a)\right]\mathbf{v}(a). \tag{3.5}$$

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

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

Lemma 3.1. *If* $\mathbf{K}(a)$ *is a constant matrix* $\mathbf{K}$*, then hypothesis* H3 *holds.*

The proof of this lemma is skipped. It is based on the use of a Lyapunov function associated with $\mathbf{K}_S$.

From (3.2), (3.4) we can obtain the function $\mathbf{q}_\varepsilon$ in terms of p_ε. Then, substituting in (3.1), (3.3) we obtain a problem for p_ε. In order to determine $\mathbf{q}_\varepsilon$ in terms of p_ε, let us consider the more general nonhomogeneous problem

$$\frac{\partial \mathbf{q}}{\partial a} + \frac{\partial \mathbf{q}}{\partial t} = \left[\frac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a)\right]\mathbf{q}(a,t) + \mathbf{F}(a,t), \tag{3.6}$$

$$\mathbf{q}(0,t) = \int_0^{+\infty} \mathbf{B}_S(a)\mathbf{q}(a,t)da + \mathbf{G}(t), \tag{3.7}$$

$$\mathbf{q}(a,0) = \mathbf{q}_0(a). \tag{3.8}$$

Lemma 3.2. *For* $\varepsilon > 0$ *small enough, there exists a function* $\boldsymbol{\Phi}_\varepsilon : \mathbf{R}_+ \longrightarrow \mathcal{L}(S)$*, differentiable for every* $a \geq 0$ *and such that*

$$\boldsymbol{\Phi}'_\varepsilon(a) = \left[\tfrac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a)\right]\boldsymbol{\Phi}_\varepsilon(a), \qquad a \geq 0,$$
$$\boldsymbol{\Phi}_\varepsilon(0) - \int_0^{+\infty}\mathbf{B}_S(a)\boldsymbol{\Phi}_\varepsilon(a)da = Id.$$

As usual, $\mathcal{L}(S)$ means the space of bounded linear operators defined on S.

Proof. The first equation is just (3.5). So, it yields the following expression for $\boldsymbol{\Phi}_\varepsilon$:

$$\boldsymbol{\Phi}_\varepsilon(a) = R_\varepsilon(a,0)\boldsymbol{\Phi}_\varepsilon(0),$$

where R_ε is the resolvent matrix introduced in Hypothesis H3. Then, we obtain for $\mathbf{\Phi}_\varepsilon(0)$ the equation

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

which has a solution for every $\varepsilon > 0$, small enough, due to the bound assumed for R_ε in Hypothesis H3. Let us notice, moreover, that $\lim_{\varepsilon\to 0_+} \mathbf{\Phi}_\varepsilon(0) = Id$. □

Now, we perform a change of the unknown function from $\mathbf{q}$ to $\mathbf{q}_1$ defined by

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

This transforms the problem (3.6)–(3.8) into another nonhomogeneous problem with a homogeneous condition for $a = 0$:

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

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

$$\frac{\partial \mathbf{q}}{\partial a} + \frac{\partial \mathbf{q}}{\partial t} = \left[\frac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a)\right] \mathbf{q}(a,t), \tag{3.9}$$

$$\mathbf{q}(0,t) = \int_0^{+\infty} \mathbf{B}_S(a)\mathbf{q}(a,t)da, \tag{3.10}$$

$$\mathbf{q}(a,0) = \mathbf{q}_0(a) - \mathbf{\Phi}_\varepsilon(a)\mathbf{G}(0). \tag{3.11}$$

To be specific,

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

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

$$\mathbf{q}_\varepsilon(\cdot,t) = \mathcal{U}_\varepsilon(t)\mathbf{q}_0(\cdot) + \int_0^t \mathcal{U}_\varepsilon(t-\tau)\mathbf{F}(\cdot,\tau)d\tau - \int_0^t \mathcal{V}_\varepsilon(t-\tau)(\cdot)\mathbf{G}(\tau)d\tau, \tag{3.12}$$

where

$$\mathcal{V}_\varepsilon(t)(a) = \left[\frac{\partial \mathcal{U}_\varepsilon}{\partial t}(t)\mathbf{\Phi}_\varepsilon\right](a), \qquad a > 0, \quad t \geq 0. \tag{3.13}$$

In our case

$$\begin{aligned}
\mathbf{F}(a,t) &= -\left[\mathbf{M}_S(a)\boldsymbol{\nu}(a) + \boldsymbol{\nu}'(a)\right] p_\varepsilon(a,t),\\
\mathbf{G}(t) &= \textstyle\int_0^{+\infty} \mathbf{B}_S(a)\boldsymbol{\nu}(a)p_\varepsilon(a,t)da.
\end{aligned}$$

Now, we substitute expression (3.12) of $\mathbf{q}_\varepsilon(\cdot,t)$ in (3.1), (3.3), obtaining the equations for $p_\varepsilon(a,t)$:

$$\frac{\partial p_\varepsilon}{\partial a}+\frac{\partial p_\varepsilon}{\partial t}=-\mu^*(a)p_\varepsilon(a,t)+(\mathcal{D}_\varepsilon(t)p_\varepsilon)(a)+f_\varepsilon(a,t)\qquad(a>0\ ,\ t>0), \tag{3.14}$$

$$p_\varepsilon(0,t)=\int_0^{+\infty}\beta^*(a)p_\varepsilon(a,t)da+\mathcal{B}_\varepsilon(t)p_\varepsilon+g_\varepsilon(t)\qquad(t>0), \tag{3.15}$$

$$p_\varepsilon(a,0)=p_0(a)\qquad(a>0), \tag{3.16}$$

where

$$f_\varepsilon(a,t)=-\mathbf{1}^{\mathsf{T}}\mathbf{M}(a)(\mathcal{U}_\varepsilon(t)\mathbf{q}_0)(a), \tag{3.17}$$

$$g_\varepsilon(t)=\int_0^{\infty}\mathbf{1}^{\mathsf{T}}\mathbf{B}(a)(\mathcal{U}_\varepsilon(t)\mathbf{q}_0)(a)da, \tag{3.18}$$

and we have defined, for each $t>0$ fixed, the following two operators:

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

$$\begin{aligned}\mathcal{D}_\varepsilon(t)\,(p)\,(a)&=\mathbf{1}^{\mathsf{T}}\mathbf{M}(a)\int_0^t\mathcal{U}_\varepsilon(t-\tau)\left[\mathbf{M}_S(a)\boldsymbol{\nu}(a)+\boldsymbol{\nu}'(a)\right]p(a,\tau)d\tau\\ &\quad+\mathbf{1}^{\mathsf{T}}\mathbf{M}(a)\int_0^t\mathcal{V}_\varepsilon(t-\tau)(a)\left(\int_0^{+\infty}\mathbf{B}_S(\alpha)\boldsymbol{\nu}(\alpha)p(\alpha,t)d\alpha\right)d\tau,\end{aligned} \tag{3.19}$$

$$\begin{aligned}\mathcal{B}_\varepsilon(t)p&=-\int_0^{+\infty}\mathbf{1}^{\mathsf{T}}\mathbf{B}(a)\left(\int_0^t\mathcal{U}_\varepsilon(t-\tau)\left[\mathbf{M}_S(a)\boldsymbol{\nu}(a)+\boldsymbol{\nu}'(a)\right]p(a,\tau)d\tau\right)da\\ &\quad-\int_0^{+\infty}\mathbf{1}^{\mathsf{T}}\mathbf{B}(a)\left(\int_0^t\mathcal{V}_\varepsilon(t-\tau)(a)\left(\int_0^{+\infty}\mathbf{B}_S(\alpha)\boldsymbol{\nu}(\alpha)p(\alpha,\tau)d\alpha\right)d\tau\right)da.\end{aligned} \tag{3.20}$$

3.1. Formulation of a fixed point problem for the function p_ε. Integrating (3.14) along characteristic lines, we can formulate this system as a fixed point problem. To this end, we need some estimates stated in the following lemmas, whose proofs are deferred to the Appendix.

Throughout the paper, we denote by C_i, $i=1,\ldots$, constants arising from computations whose specific value is not important.

LEMMA 3.3. *The semigroup $\{\mathcal{U}_\varepsilon(t)\}_{t\geq 0}$ satisfies the following estimate:*

$$\|\mathcal{U}_\varepsilon(t)\|\leq C_1e^{(C_2-k_1/\varepsilon)t}\qquad(t\geq 0),$$

where k_1 is the same as in Hypothesis H3.

LEMMA 3.4. *For each $t\geq 0$, the function $\mathcal{V}_\varepsilon(t)(\cdot):\mathbf{R}_+\longrightarrow\mathcal{L}(\mathbf{R}^N)$ defined in* (3.13), *satisfies the following estimate:*

$$\|\mathcal{V}_\varepsilon(t)\|_{L^1}\leq C_1e^{(C_2-k_1/\varepsilon)t}.$$

LEMMA 3.5. *For each $t \geq 0$, the operators $\mathcal{D}_\varepsilon(t)$ and $\mathcal{B}_\varepsilon(t)$ defined in* (3.19), (3.20) *satisfy the following estimates:*

$$\|\mathcal{D}_\varepsilon(t)p\|_{L^1(\mathbf{R}_+)} \leq \varepsilon C_1 \sup_{\tau\in[0,t]} \|p(\cdot,\tau)\|_{L^1},$$

$$|\mathcal{B}_\varepsilon(t)p| \leq \varepsilon C_2 \sup_{\tau\in[0,t]} \|p(\cdot,\tau)\|_{L^1}.$$

We now return to system (3.14)–(3.16).

Denote by $\rho_0(a,\alpha)$, $\rho_0(\alpha,\alpha)=1$, the resolvent operator of the problem

$$\frac{dz}{da} = -\mu^*(a)z(a).$$

Observe that $\rho_0(a,0) = e^{-\int_0^a \mu^*(s)\,ds}$ is the resolvent function associated with the aggregated problem (2.10)–(2.12). After standard calculations, we obtain

(i) for $a > t$:

$$\begin{aligned} p_\varepsilon(a,t) &= \rho_0(a,a-t)p_0(a-t) \\ &\quad + \int_0^t \rho_0(a,a-t+\sigma)\left[(\mathcal{D}_\varepsilon(\sigma)p_\varepsilon)(a-t+\sigma) + f_\varepsilon(a-t+\sigma,\sigma)\right]d\sigma. \end{aligned} \tag{3.21}$$

(ii) for $a < t$:

$$\begin{aligned} p_\varepsilon(a,t) &= \rho_0(a,0)\left[\int_0^{+\infty} \beta^*(\alpha)p_\varepsilon(\alpha,t-a)d\alpha + \mathcal{B}_\varepsilon(t-a)p_\varepsilon + g_\varepsilon(t-a)\right] \\ &\quad + \int_0^a \rho_0(a,\sigma)\left[(\mathcal{D}_\varepsilon(t-a+\sigma)p_\varepsilon)(\sigma) + f_\varepsilon(\sigma,t-a+\sigma)\right]d\sigma. \end{aligned} \tag{3.22}$$

Both (3.21) and (3.22) can be reformulated as a single equation of the form

$$p_\varepsilon = \mathcal{F}(\varepsilon, p_\varepsilon), \tag{3.23}$$

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

(i) A term $\mathcal{H}_0$, independent of ε:

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

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

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

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

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

We have

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

In order to apply a fixed point theorem, we consider for $T > 0$ the Banach space $C = C([0,T]; L^1(\mathbf{R}_+))$, with the norm

$$\|p\|_C = \sup_{[0,T]} \|p(\cdot, t)\|_{L^1(\mathbf{R}_+)}.$$

LEMMA 3.6. *Under the hypothesis* $\mu_* > \tilde{\beta}^* = \sup_{a\geq 0} \beta^*(a)$*, the equation*

$$(Id - \mathcal{H}_0)p = \Phi$$

has, for each $\Phi \in C$*, a unique solution* $p \in C$*.*

The proof of this lemma is skipped. It can be done by showing that $\mathcal{H}_0$ is a strict contraction when restricted to a suitable function space.

Notice that the hypothesis $\mu_* > \tilde{\beta}^*$ does not introduce any restriction in the model. In fact, performing in (2.1)–(2.3) the change of unknown (if necessary)

$$\mathbf{n}^*(a,t) = e^{-mt}\mathbf{n}(a,t)$$

for some $m > \tilde{\beta}^* - \mu_*$, we obtain an equivalent model in which the condition of Lemma 3.6 is accomplished.

From Lemmas 3.3–3.5, after some straightforward calculations, we obtain the following estimate for the operator $\mathcal{A}(\varepsilon, \cdot)$:

$$\|\mathcal{A}(\varepsilon, p)\|_C \leq C_1 \frac{\varepsilon}{\mu_*} \|p\|_C. \tag{3.24}$$

Lemma 3.6 establishes the existence of the inverse $(Id - \mathcal{H}_0)^{-1}$. The following estimate can be obtained:

$$\|(Id - \mathcal{H}_0)^{-1}\| \leq \frac{2\mu_*}{\mu_* - \tilde{\beta}^*}.$$

Then, bearing in mind (3.24), we can ensure the existence of the inverse $(Id - \mathcal{H}_0 - \mathcal{A}(\varepsilon, \cdot))^{-1}$, for $\varepsilon > 0$ small enough:

$$(Id - \mathcal{H}_0 - \mathcal{A}(\varepsilon, \cdot))^{-1} = (Id - \mathcal{H}_0)^{-1} + \Gamma_\varepsilon,$$

where

$$\Gamma_\varepsilon = \left[\sum_{j\geq 1} \left[(Id - \mathcal{H}_0)^{-1} \mathcal{A}(\varepsilon, \cdot) \right]^j \right] (Id - \mathcal{H}_0)^{-1}$$

with

$$\|\Gamma_\varepsilon(p)\|_C \leq \varepsilon C_1 \|p\|_C.$$

We can then write the following expression for the solution p_ε of (3.23):

$$p_\varepsilon = (Id - \mathcal{H}_0 - \mathcal{A}(\varepsilon, \cdot))^{-1}[\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)] = \left[(Id - \mathcal{H}_0)^{-1} + \Gamma_\varepsilon \right] [\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)]. \tag{3.25}$$

3.2. Asymptotic expression for the perturbed semigroup. We are going to study the dependence on ε of the solution p_ε obtained in (3.25). This solution, together with the expression for $\mathbf{q}_\varepsilon$ obtained by substituting p_ε in (3.12), gives the solution $\mathbf{n}_\varepsilon$ of the perturbed problem (2.1)–(2.3).

Let us define

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

In the Appendix the following lemma is proved.

LEMMA 3.7. *$\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0) = \mathcal{J}(0, p_0, \mathbf{0}) + \varepsilon \tilde{B}(\varepsilon, p_0, \mathbf{q}_0)$, where*

$$\|\tilde{B}(\varepsilon, p_0, \mathbf{q}_0)(\cdot, t)\|_{L^1(\mathbf{R}_+)} \le C_1 e^{-\mu_* t} \|\mathbf{q}_0\|_{L^1(\mathbf{R}_+)} \quad (t \ge 0).$$

Straightforward calculations lead to the following asymptotic expression for p_ε:

$$p_\varepsilon = [Id - \mathcal{H}_0]^{-1} \left(\mathcal{J}(0, p_0, \mathbf{0})\right) + \varepsilon B(\varepsilon, p_0, \mathbf{q}_0), \tag{3.26}$$

where B is an operator defined by formula (3.26) and satisfies, for some constant $C_1 > 0$,

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

The term $(Id - \mathcal{H}_0)^{-1}[\mathcal{J}(0, p_0, \mathbf{0})]$ is the solution of (3.14) and (3.15) for $\varepsilon = 0$, which is just the aggregated model (2.10), (2.11), with initial age distribution $p_0(a)$. Then, it can be expressed in terms of the semigroup $\{S_0(t)\}_{t \ge 0}$, as $S_0(t)p_0$.

Remember that the solution of perturbed problem (2.1)–(2.3) can be written as

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

where p_ε is given by (3.25) and $\mathbf{q}_\varepsilon$ is given by (3.12). Both results, together with (3.26), give finally

$$\mathbf{n}_\varepsilon(a,t) = \left(S_0(t)p_0\right)(a)\boldsymbol{\nu}(a) + \left(\mathcal{U}_\varepsilon(t)\mathbf{q}_0\right)(a) + \varepsilon B(\varepsilon, p_0, \mathbf{q}_0)(a,t)\boldsymbol{\nu}(a) + \mathbf{Q}_\varepsilon(a,t), \tag{3.27}$$

where

$$\|\mathbf{Q}_\varepsilon(\cdot, t)\|_{L^1(\mathbf{R}_+)} \le \varepsilon C_1 e^{(C_2 - k_1/\varepsilon)t}.$$

The main result of this section is summarized in the following theorem.

THEOREM 3.8. *For every $\varepsilon > 0$, small enough,*

$$\begin{aligned}(T_\varepsilon(t)\boldsymbol{\phi})(a) &= \left(S_0(t)p_0\right)(a)\boldsymbol{\nu}(a) + (\mathcal{U}_\varepsilon(t)\mathbf{q}_0)(a) \\ &+ \varepsilon B(\varepsilon, p_0, \mathbf{q}_0)(a,t)\boldsymbol{\nu}(a) + O\left(\varepsilon e^{(C_1 - k_1/\varepsilon)t}\right),\end{aligned}$$

where $\{S_0(t)\}_{t \ge 0}$ is the semigroup associated with the aggregated model (2.10)–(2.12) *and $\boldsymbol{\phi} = p_0\boldsymbol{\nu} + \mathbf{q}_0$, with $\mathbf{q}_0 \in S$, is the initial age distribution.*

We point out that the above formula is of interest mainly in the case when $\lambda_0 \ge 0$. In this case, it can be concluded from the formula that

$$T_\varepsilon(t)\boldsymbol{\phi} \approx S_0(t)p_0 \otimes \boldsymbol{\nu} \quad \text{as } t \longrightarrow +\infty,$$

uniformly with respect to $\varepsilon > 0$ small enough. Conversely, if $\lambda_0 < 0$, then

$$T_\varepsilon(t)\boldsymbol{\phi} \longrightarrow 0 \quad \text{as } t \longrightarrow +\infty,$$

and this is again uniform with respect to $\varepsilon > 0$ small enough. In this case, however, $S_0(t)p_0 \otimes \boldsymbol{\nu}$ does not, in general, dominate the term εB.

COROLLARY 3.9. *For each $t > 0$, we have*

$$\lim_{\varepsilon \to 0} T_\varepsilon(t)\boldsymbol{\phi} = S_0(t)p_0\boldsymbol{\nu}, \tag{3.28}$$

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

In order for the solution to reach the unperturbed state, it is necessary that the migration between patches equilibrate the proportions in the various patches according to the vector $\boldsymbol{\nu}$. This implies that the newborns, which are produced in proportions unrelated to $\boldsymbol{\nu}$, move between patches until the proportion $\boldsymbol{\nu}$ is reached. The process takes a time of the order of ε.

4. Asymptotic exponential growth of the perturbed semigroup. In this section we will show that the semigroup $\{T_\varepsilon(t)\}_{t\geq 0}$ has the asynchronous exponential growth property. We also obtain the behavior of its associated malthusian parameter λ_ε and eigenfunction $\boldsymbol{\varphi}_\varepsilon$ as $\varepsilon \to 0$: λ_ε converges to λ_0 and $\boldsymbol{\varphi}_\varepsilon$ converges to $\theta_0\boldsymbol{\nu}$, where λ_0, respectively, θ_0, is the malthusian parameter, respectively, the asymptotic distribution, associated with the aggregated model (2.10)–(2.12).

4.1. The spectrum of the infinitesimal generator $\boldsymbol{A_\varepsilon}$. With the aim of finding the spectrum of A_ε, $\sigma(A_\varepsilon)$, and its dependence on ε, we solve the equation

$$(A_\varepsilon - \lambda I)\boldsymbol{\varphi} = \mathbf{0}, \quad \boldsymbol{\varphi} \in D(A_\varepsilon), \tag{4.1}$$

by decomposing the solution into its stable and unstable parts.

To simplify the notation we make the following change in the unknown function:

$$\boldsymbol{\varphi}(a) = e^{-\lambda a}\boldsymbol{\varphi}_\lambda(a).$$

From Hypothesis H1 we can write the following direct sum decomposition:

$$\mathbf{R}^N = [\boldsymbol{\nu}(a)] \oplus S$$

and then we can decompose $\boldsymbol{\varphi}_\lambda$ into

$$\boldsymbol{\varphi}_\lambda(a) = \theta_\lambda(a)\boldsymbol{\nu}(a) + \boldsymbol{\sigma}_\lambda(a) \qquad \boldsymbol{\sigma}_\lambda(a) \in S.$$

By substituting in (4.1) and having in mind that $\mathbf{K}(a)\boldsymbol{\nu}(a) = \mathbf{0}$, we obtain

$$\theta'_\lambda(a)\boldsymbol{\nu}(a) + \theta_\lambda(a)\boldsymbol{\nu}'(a) + \boldsymbol{\sigma}'_\lambda(a) = -\theta_\lambda(a)\mathbf{M}(a)\boldsymbol{\nu}(a) - \mathbf{M}(a)\boldsymbol{\sigma}_\lambda(a) + \frac{1}{\varepsilon}\mathbf{K}(a)\boldsymbol{\sigma}_\lambda(a).$$

We project onto subspaces $[\boldsymbol{\nu}(a)]$ and S and, since $\boldsymbol{\sigma}'(a) \in S$ for each a, we obtain the following system for the components of $\boldsymbol{\varphi}_\lambda$:

$$\theta'_\lambda(a) = -\mu^*(a)\theta_\lambda(a) - \mathbf{1}^{\mathsf{T}}\mathbf{M}(a)\boldsymbol{\sigma}_\lambda(a), \tag{4.2}$$

$$\boldsymbol{\sigma}'_\lambda(a) = \left[\frac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a)\right]\boldsymbol{\sigma}_\lambda(a) - \left[\mathbf{M}_S(a)\boldsymbol{\nu}(a) + \boldsymbol{\nu}'(a)\right]\theta_\lambda(a). \tag{4.3}$$

The general solution of that system can be expressed in terms of the resolvent operator $R_\varepsilon(a,\alpha)$ introduced in Hypothesis H3. Applying a variation of constants formula, we can get an expression for $\boldsymbol{\sigma}_\lambda(a)$ in terms of θ_λ:

$$\boldsymbol{\sigma}_\lambda(a) = R_\varepsilon(a,0)\boldsymbol{\sigma}_\lambda(0) - \int_0^a R_\varepsilon(a,\alpha)\left[\mathbf{M}_S(\alpha)\boldsymbol{\nu}(\alpha) + \boldsymbol{\nu}'(\alpha)\right]\theta_\lambda(\alpha)d\alpha \tag{4.4}$$

and substituting in (4.2) we obtain an integrodifferential equation for $\theta_\lambda(a)$,

$$\theta_\lambda'(a) = -\mu^*(a)\theta_\lambda(a) + \int_0^a r_\varepsilon(a,\alpha)\theta_\lambda(\alpha)d\alpha - \mathbf{1}^\mathsf{T}\mathbf{M}(a)R_\varepsilon(a,0)\boldsymbol{\sigma}_\lambda(0), \tag{4.5}$$

where we have used the notation

$$r_\varepsilon(a,\alpha) = \mathbf{1}^\mathsf{T}\mathbf{M}(a)R_\varepsilon(a,\alpha)\left[\mathbf{M}_S(\alpha)\boldsymbol{\nu}(a) + \boldsymbol{\nu}'(a)\right].$$

Let us notice that

$$|r_\varepsilon(a,\alpha)| \le C_1 e^{(k_2-k_1/\varepsilon)(a-\alpha)},\ a \ge \alpha. \tag{4.6}$$

Let $\rho_\varepsilon(a,\alpha)$, $a \ge \alpha$, with $\rho_\varepsilon(\alpha,\alpha) = 1$, be the resolvent kernel of the homogeneous integral equation

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

In terms of $\rho_\varepsilon(a,\alpha)$, the solution of (4.5) reads

$$\theta_\lambda(a) = \rho_\varepsilon(a,0)\theta_\lambda(0) - \left[\int_0^a \rho_\varepsilon(a,\alpha)\mathbf{1}^\mathsf{T}\mathbf{M}(\alpha)R_\varepsilon(\alpha,0)d\alpha\right]\boldsymbol{\sigma}_\lambda(0)$$

which, substituted in (4.4), yields the following expression for the solution of the system (4.2), (4.3):

$$\theta(a) = e^{-\lambda a}\rho_\varepsilon(a,0)\theta(0) + e^{-\lambda a}\boldsymbol{\xi}_\varepsilon^\mathsf{T}(a)\boldsymbol{\sigma}(0), \tag{4.7}$$

$$\boldsymbol{\sigma}(a) = e^{-\lambda a}\boldsymbol{\eta}_\varepsilon(a)\theta(0) + e^{-\lambda a}\boldsymbol{\Lambda}_\varepsilon(a)\boldsymbol{\sigma}(0), \tag{4.8}$$

where

$$\begin{aligned}
\boldsymbol{\xi}_\varepsilon^\mathsf{T}(a) &= \int_0^a \rho_\varepsilon(a,\alpha)\mathbf{1}^\mathsf{T}\mathbf{M}(\alpha)R_\varepsilon(\alpha,0)d\alpha,\\
\boldsymbol{\eta}_\varepsilon(a) &= \int_0^a R_\varepsilon(a,\alpha)\left[\mathbf{M}_S(\alpha)\boldsymbol{\nu}(\alpha) + \boldsymbol{\nu}'(\alpha)\right]\rho_\varepsilon(\alpha,0)d\alpha,\\
\boldsymbol{\Lambda}_\varepsilon(a) &= R_\varepsilon(a,0) + \int_0^a R_\varepsilon(a,\alpha)\left[\mathbf{M}_S(\alpha)\boldsymbol{\nu}(\alpha) + \boldsymbol{\nu}'(\alpha)\right]\boldsymbol{\xi}_\varepsilon^\mathsf{T}(a)d\alpha,
\end{aligned}$$

and we have returned to the notation

$$\theta(a) = e^{\lambda a}\theta_\lambda(a); \quad \boldsymbol{\sigma}(a) = e^{-\lambda a}\boldsymbol{\sigma}_\lambda(a).$$

4.2. Characteristic equation. From the definition (2.6) of the infinitesimal generator A_ε, through standard calculations, we obtain the following characteristic equation for its eigenvalues $\lambda \in \sigma(A_\varepsilon)$:

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

Another expression for this characteristic equation can be obtained from (4.7), (4.8) by substituting $\boldsymbol{\varphi}(a) = \theta(a)\boldsymbol{\nu}(a) + \boldsymbol{\sigma}(a)$ in the birth equation

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

which yields, in matrix form,

$$\begin{pmatrix} \theta(0) \\ \boldsymbol{\sigma}(0) \end{pmatrix} = \begin{pmatrix} d_1(\varepsilon,\lambda) & \mathbf{d}_2^{\mathsf{T}}(\varepsilon,\lambda) \\ \mathbf{d}_3(\varepsilon,\lambda) & \mathbf{D}_4(\varepsilon,\lambda) \end{pmatrix} \begin{pmatrix} \theta(0) \\ \boldsymbol{\sigma}(0) \end{pmatrix},$$

where

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

We deduce from the last equality that the elements $\lambda_\varepsilon \in \sigma(A_\varepsilon)$ are the solutions of the characteristic equation

$$\det \begin{bmatrix} d_1(\varepsilon,\lambda) - 1 & \mathbf{d}_2^{\mathsf{T}}(\varepsilon,\lambda) \\ \mathbf{d}_3(\varepsilon,\lambda) & \mathbf{D}_4(\varepsilon,\lambda) - \mathbf{I} \end{bmatrix} = 0. \tag{4.9}$$

To prove the existence of real solutions of the characteristic equation (4.9) we need a bound for the resolvent kernel $\rho_\varepsilon(a,\alpha)$ that we state in the following lemma.

LEMMA 4.1. *For $\varepsilon > 0$ small enough, it is verified that*

$$|\rho_\varepsilon(a,\alpha)| \le e^{-k_M(a-\alpha)} + \varepsilon C_1 e^{\varepsilon C_2(a-\alpha)}, \ a \ge \alpha, \tag{4.10}$$

where k_M is any constant for which $0 < k_M < \mu_*$ holds.

Proof. For the proof, see the Appendix.

PROPOSITION 4.2. *Recall that $\rho_0(a,0) = e^{-\int_0^a \mu^*(s)ds}$. Then we have*

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

uniformly for $a \ge 0$.

Proof. For the proof, see the Appendix.

COROLLARY 4.3. *There exists $\varepsilon_0 > 0$ such that for each $a \ge 0$, $\rho_\varepsilon(a,0) > 0$ holds for every $0 < \varepsilon < \varepsilon_0$.*

We can now prove the existence of real solutions of (4.9) which are elements of $\sigma(A_\varepsilon)$ as close as needed to the root λ_0 of (2.13).

PROPOSITION 4.4. *Let λ_0 be the unique real solution of* (2.13)*. For any $\delta > 0$ such that $-\mu_* < \lambda_0 - \delta$, there exists $\varepsilon_0(\delta) > 0$ such that for every $0 < \varepsilon < \varepsilon_0(\delta)$, the characteristic equation* (4.9) *possesses at least a real solution $\lambda_\varepsilon \in [\lambda_0 - \delta, \lambda_0 + \delta]$.*

Proof. From Hypothesis H3 and Lemma 4.1 it is straightforward to obtain, for a fixed $\delta > 0$, that

$$\sup_{\lambda > \lambda_0 - \delta} \|\mathbf{D}_4(\varepsilon, \lambda)\| \longrightarrow 0 \qquad (\varepsilon \to 0_+)$$

and therefore there exists $\varepsilon_0(\delta) > 0$ such that for every $\lambda > \lambda_0 - \delta$ and every $\varepsilon \in]0, \varepsilon_0[$, $\|\mathbf{D}_4(\varepsilon, \lambda)\| < 1$ holds. This allows us to write

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

and substituting it in the expression of $\theta(0)$ we have

$$\theta(0) = d_1(\varepsilon, \lambda)\theta(0) + \mathbf{d}_2^{\mathsf{T}}(\varepsilon, \lambda)(\mathbf{I} - \mathbf{D}_4(\varepsilon, \lambda))^{-1} \mathbf{d}_3(\varepsilon, \lambda)\theta(0)$$

which, in view of the expression of d_1, yields that

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

where

$$\begin{aligned} \sigma(\varepsilon, \lambda) \quad = \quad & \textstyle\int_0^{+\infty} e^{-\lambda a} \beta^*(a)(\rho_\varepsilon(a, 0) - \rho_0(a, 0) da) + \int_0^{+\infty} e^{-\lambda a} \mathbf{1}^{\mathsf{T}} \mathbf{B}(a) \boldsymbol{\eta}_\varepsilon(a) da \\ & + \mathbf{d}_2^{\mathsf{T}}(\varepsilon, \lambda)(\mathbf{I} - \mathbf{D}_4(\varepsilon, \lambda))^{-1} \mathbf{d}_3(\varepsilon, \lambda). \end{aligned}$$

Straightforward computations lead to

$$\sup_{\lambda > \lambda_0 - \delta} |\sigma(\varepsilon, \lambda)| \longrightarrow 0 \qquad (\varepsilon \to 0_+).$$

Now, if we call

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

in view of (2.13), we have that there exists $\varepsilon_0 > 0$, $\varepsilon_0 = \varepsilon_0(\delta)$, such that

$$G(\varepsilon, \lambda_0 - \delta) > 1 > G(\varepsilon, \lambda_0 + \delta) \quad \text{for every } \varepsilon \in]0, \varepsilon_0(\delta)[$$

which implies the existence of a real root, $\lambda_\varepsilon \in [\lambda_0 - \delta, \lambda_0 + \delta]$, of the equation $G(\varepsilon, \lambda_\varepsilon) = 1$, which is, therefore, a root of the characteristic equation (4.9). ◻

4.3. Asynchronous exponential growth of the perturbed semigroup. We cannot deduce immediately that the eigenvalue λ_ε, whose existence has been proved in Proposition 4.4, is equal to the spectral bound $s(A_\varepsilon)$ of the infinitesimal generator A_ε. In order to prove the equality, we establish in the following proposition the asynchronous exponential growth property for the perturbed semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$. This property is a consequence of essential compactness and irreducibility of $\{T_\varepsilon(t)\}_{t \geq 0}$ for $\varepsilon > 0$ small enough. Irreducibility makes it necessary to impose an additional assumption on the fertility rate function.

HYPOTHESIS H4. *There exists $a_1 > 0$ such that for all $a > a_1$, $\|B(a)\| > 0$.*

PROPOSITION 4.5. *Under Hypothesis* H4, *the semigroup* $\{T_\varepsilon(t)\}_{t\geq 0}$ *is irreducible and, for* $\varepsilon > 0$ *small enough, is essentially compact.*

Proof. For the proof, see the Appendix.

Straightforward calculations show that the characteristic equation (4.9) has a unique positive real root which is strictly dominant. Thus, (see [1], [3], [23]), we can conclude from Propositions 4.4 and 4.5, that $s(A_\varepsilon) = \lambda_\varepsilon$.

The eigenfunction $\boldsymbol{\varphi}_\varepsilon(a) = \theta_\varepsilon(a)\,\boldsymbol{\nu}(a) + \boldsymbol{\sigma}_\varepsilon(a)$ associated with λ_ε verifies the following asymptotic result.

PROPOSITION 4.6. *Let* λ_ε *be the eigenvalue of* A_ε *found in Proposition* 4.4. *Then, there exists an eigenfunction,* $\boldsymbol{\varphi}_\varepsilon(a)$, *associated with* λ_ε *which verifies*

$$\lim_{\varepsilon\to 0_+} \boldsymbol{\varphi}_\varepsilon(a) = \theta_0(a)\boldsymbol{\nu}(a), \quad a \geq 0,$$

where $\theta_0(a) = e^{-\lambda_0 a}\rho_0(a,0)$. *In particular, for every* $\varepsilon > 0$ *small enough,* $\boldsymbol{\varphi}_\varepsilon(a) > \mathbf{0}$, $(a > 0)$.

Proof. From expressions (4.7), (4.8), we have

$$\begin{aligned}\boldsymbol{\varphi}_\varepsilon(a) &= \theta_\varepsilon(a)\boldsymbol{\nu}(a) + \boldsymbol{\sigma}_\varepsilon(a)\\ &= \left(e^{-\lambda_\varepsilon a}\rho_\varepsilon(a,0)\theta(0) + e^{-\lambda_\varepsilon a}\boldsymbol{\xi}_\varepsilon^{\mathsf{T}}(a)\boldsymbol{\sigma}(0)\right)\boldsymbol{\nu}(a) + e^{-\lambda_\varepsilon a}\boldsymbol{\eta}_\varepsilon(a)\theta(0) + e^{-\lambda_\varepsilon a}\boldsymbol{\Lambda}_\varepsilon(a)\boldsymbol{\sigma}(0).\end{aligned}$$

If we choose $\theta(0) = 1$ we obtain from the proof of Proposition 4.4 that $\boldsymbol{\sigma}(0) = (\mathbf{I} - \mathbf{D}_4(\varepsilon,\lambda_\varepsilon))^{-1}\mathbf{d}_3(\varepsilon,\lambda_\varepsilon)$, and hence

$$\begin{aligned}\boldsymbol{\varphi}_\varepsilon(a) &= e^{-\lambda_\varepsilon a}\rho_\varepsilon(a,0)\boldsymbol{\nu}(a) + e^{-\lambda_\varepsilon a}\boldsymbol{\eta}_\varepsilon(a)\\ &\quad + \left(\boldsymbol{\nu}(a)e^{-\lambda_\varepsilon a}\boldsymbol{\xi}_\varepsilon^{\mathsf{T}}(a) + e^{-\lambda_\varepsilon a}\boldsymbol{\Lambda}_\varepsilon(a)\right)(\mathbf{I} - \mathbf{D}_4(\varepsilon,\lambda_\varepsilon))^{-1}\mathbf{d}_3(\varepsilon,\lambda_\varepsilon).\end{aligned}$$

The use of the different bounds obtained above leads us to the final result:

$$\lim_{\varepsilon\to 0_+} \boldsymbol{\varphi}_\varepsilon(a) = e^{-\lambda_0 a}\rho_0(a,0)\boldsymbol{\nu}(a) = e^{-\lambda_0 a}e^{-\int_0^a \mu^*(s)ds}\boldsymbol{\nu}(a). \qquad \square$$

The following theorem summarizes the results obtained in this section.

THEOREM 4.7. *For every* $\varepsilon > 0$ *small enough, it is verified that*

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

where $\mathbf{n}_\varepsilon(a,t)$ *is the solution of* (2.1)–(2.3), λ_ε *is the real solution of the characteristic equation* (4.9), $\boldsymbol{\varphi}_\varepsilon(a) = \theta_\varepsilon(a)\boldsymbol{\nu}(a)+\boldsymbol{\sigma}_\varepsilon(a)$ *is the eigenfunction expressed in Proposition* 4.6, *and* $C_\varepsilon(\boldsymbol{\phi})$ *is a positive constant depending on the initial age distribution* $\boldsymbol{\phi}$. *Moreover,*

$$\lim_{\varepsilon\to 0_+} \lambda_\varepsilon = \lambda_0$$

and

$$\lim_{\varepsilon\to 0_+} \boldsymbol{\varphi}_\varepsilon(a) = e^{\lambda_0 a}e^{-\int_0^a \mu^*(\sigma)d\sigma}\boldsymbol{\nu}(a).$$

5. Conclusion. The present work explores the important class of age-structured population models, with continuous age-structure, and a lattice spatial structure. More specifically, it is assumed that the population occupies some space subdivided into N patches: individuals may migrate from patch to patch according to a spatial transition matrix; they also reproduce, age, and die. It is also assumed that the migration process is much faster than the demographic (birth, death, and aging) process. How fast it is, is marked by the presence of a multiplicative constant $R = 1/\varepsilon$ before a normalized transition matrix $\mathbf{K}$, where ε can be interpreted as the time needed for a single patch migration of a single individual. A crucial assumption is that the jump process is conservative with respect to the life dynamics of the population, that is to say, no death or birth is directly incurred by spatial migrations. This is reflected in the coefficients of the transition matrix: on a given column, off-diagonal coefficients are proportions of the individuals of the given patch which migrate to other patches, and are thus positive, while the diagonal coefficient represents the resulting loss from the given patch, and is thus negative. The sum of the coefficients of any given column of the transition matrix is equal to zero. Under two additional assumptions on $\mathbf{K}$, (1) it should be irreducible, and (2) an assumption about the flow associated with a sort of a projection of the main equation onto the space of transients, (the latter assumption is to be made only in the case when the transition matrix is not constant from some age on), and under an assumption on the fertility rate function, the following two results have been shown:

(A) Exponential asynchronous growth with asymptotic expression with respect to ε, near $\varepsilon = 0$ (Theorem 4.7). Roughly speaking, we show that for $\varepsilon > 0$ small enough, each solution $\mathbf{n}_\varepsilon(a,t)$ of the perturbed system is such that

$$\mathbf{n}_\varepsilon(a,t) \sim Ce^{\lambda_\varepsilon t}\boldsymbol{\varphi}_\varepsilon(a) \qquad (t \to +\infty)$$

and λ_ε, $\boldsymbol{\varphi}_\varepsilon$ converge as $\varepsilon \to 0$:

$$\lim_{\varepsilon\to 0} \lambda_\varepsilon = \lambda_0; \quad \lim_{\varepsilon\to 0} \boldsymbol{\varphi}_\varepsilon = \boldsymbol{\nu}\theta_0,$$

where λ_0 and θ_0 are, respectively, the Malthus parameter and the associated eigenfunction of the so-called aggregated system (2.10)–(2.12) and $\boldsymbol{\nu}$ is a positive vector of the kernel of matrix $\mathbf{K}$.

(B) Nature of the convergence to the solutions of the aggregated system (Theorem 3.8). There exists a decomposition of the space $\mathbf{R}^N$ into a direct sum $\mathbf{R}^N = [\boldsymbol{\nu}(a)] \oplus S$, where $\boldsymbol{\nu}(a)$ is, for each a, the solution of $\mathbf{K}(a)\boldsymbol{\nu}(a) = \mathbf{0}$ normalized by the condition $\boldsymbol{\nu}(a) \geq \mathbf{0}$, $\|\boldsymbol{\nu}(a)\| = 1$. Accordingly, there exists a decomposition of the space of initial values $L^1(\mathbf{R}^+, \mathbf{R}^N)$ into $\big(L^1(\mathbf{R}^+, \mathbf{R}) \otimes \boldsymbol{\nu}(\cdot)\big) \oplus L^1(\mathbf{R}^+, S) = P_0 \oplus Q_0$ such that, denoting by $\{T_\varepsilon(t)\}_{t\geq 0}$ the semigroup corresponding to the value ε of the minimal transition time, for each $\boldsymbol{\phi} \in L^1(\mathbf{R}^+, \mathbf{R}^N)$, it holds that

$$(*) \qquad (T_\varepsilon(t)\boldsymbol{\phi})\,(a) = (S_0(t)p_0)\,(a)\boldsymbol{\nu}(a) + (\mathcal{U}_\varepsilon(t)\mathbf{q}_0)\,(a) + O(\varepsilon).$$

In the above formula, we have $\boldsymbol{\phi} = (p_0, \mathbf{q}_0) \in P_0 \oplus Q_0$; $\{S_0(t)\}_{t\geq 0}$ is a C_0-semigroup on $L^1(\mathbf{R}^+, \mathbf{R})$, independent of ε; $\mathcal{U}_\varepsilon(t) \in \mathcal{L}(Q_0)$ is such that

$$(**) \qquad \|\mathcal{U}_\varepsilon(t)\| \leq C_3 e^{(C_2 - C_1/\varepsilon)t}$$

for all $t \geq 0$, and some positive constants C_1, C_2, and C_3. Finally, the term $O(\varepsilon)$ denotes a bounded linear operator on $L^1(\mathbf{R}^+, \mathbf{R}^N)$, with

$$(***) \qquad \|O(\varepsilon)\|_{\mathcal{L}(L^1(\mathbf{R}^+, \mathbf{R}^N))} \leq C\varepsilon.$$

Let us now interpret formula (*). For each a, the components of $\boldsymbol{\nu}(a)$ are positive and sum up to one. They represent a distribution of individuals of age a in the patches. $(S_0(t)p_0)(a)$ gives the total number of individuals of age a. Hypotheses H1 and H2 ensure that the semigroup $\{S_0(t)\}_{t\geq 0}$ has an asynchronous exponential growth. For each $t > 0$, formula (*) yields that $T_\varepsilon(t)\boldsymbol{\phi} \to (S_0(t)p_0)\boldsymbol{\nu}$, in L^1, as $\varepsilon \to 0$. However, the convergence is not uniform in t. In fact, we have

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

Thus, the convergence is uniform with respect to t, provided that t stays far from 0, that is, for each $b > 0$, convergence is uniform in the interval $[b, +\infty[$. The convergence is definitely nonuniform on $[0,\infty[$ since $T_\varepsilon(0)\boldsymbol{\phi} = \boldsymbol{\phi} \to \boldsymbol{\phi}$ as $\varepsilon \to 0$, while if the other limit were reached uniformly on $[0, +\infty[$, we would have $T_\varepsilon(0)\boldsymbol{\phi} \to p_0\boldsymbol{\nu}$, which implies $\boldsymbol{\phi} = p_0\boldsymbol{\nu}$.

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 $\mathbf{K}(a)\mathbf{n}(a,t) = 0$, 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 the individuals to jump between two patches. Formula (*) tells us how long it takes for a given distribution to reach a neighborhood of the asymptotic distribution. It yields the following: For every $0 < \eta < (C_1/C_2)$, there exists $\kappa > 0$ such that for every $0 < \varepsilon < \eta/(C+1)$ and $t \geq \kappa\epsilon$, and every initial value $\boldsymbol{\phi}$, we have

$$\|T_\varepsilon(t)\boldsymbol{\phi} - S_0(t)p_0\boldsymbol{\nu}\| \leq \eta\|\boldsymbol{\phi}\|,$$

where C_1, C_2 are given in (**) and C is given in (***).

The solution $S_0(t)p_0\boldsymbol{\nu}$ 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.

Thus, the present work deals with singular perturbation in a semigroup setting. Our work is close in spirit to one by Khasminskii, Yin, and Zhang [16], although the equation considered in [16] is an ordinary differential equation with time-dependent coefficients. The matrix defining the equation is singular, as our transition matrix $\mathbf{K}$, with the same right eigenvector for all time t. It is also weakly irreducible in the sense that for each time t, there is a unique left eigenvector. Our results are not so precise as in [16] regarding the expansion in terms of the singular parameter. They focus more on the population dynamics relevance of our findings and are satisfactory at this level.

Let us conclude with the application of our work to fisheries. What can the aggregation method add to our knowledge of a fishery, and in particular, can aggregation show more than a crude age-dependent model of population dynamics, which does not take vertical position into account? In the case of the anchovy of the Bay of Biscay, we showed in subsection 2.3 that, starting from a vertical structure of the demographic parameters, one can aggregate these parameters along the vertical structure to arrive at an age-only dependent model which approximates reasonably well the full model. Moreover, from the general theory presented in sections 3 and 4, the discrepancy between the full model and the aggregated one can be estimated.

Thus, aggregation in our example provides a theoretical ground for the building up of an age-only dependent model, a global model which embodies some supposedly crucial migration mechanisms. In a sense, the aggregated model emerges from the full model, as a summary of the latter one, and one can expect that it captures some of the features of the full model, more than what we call a crude model, usually based on some input–output phenomenological relationships. At the same time, an aggregated model will be easier to deal with than the full model, since it has one or several variables less. As already mentioned, the restriction of spatial dependence to the vertical structure was dictated by our intent to render this paper more readable by a larger audience. We are currently working to eliminate this restriction.

6. Appendix.

Proof of Lemma 3.3. Remember that $\{\mathcal{U}_\varepsilon(t)\}_{t\geq 0}$ is the semigroup associated with the problem (3.9)–(3.11), and then, for each initial condition $\mathbf{q}_0 \in L^1(\mathbf{R}_+;\mathbf{R}^N)$, $\mathcal{U}_\varepsilon(t)\mathbf{q}_0$ is the solution $\mathbf{q}(\cdot,t)$ of this problem. Solving the system (3.9)–(3.11), along the characteristic lines, this solution can be expressed also in terms of the resolvent R_ε introduced in Hypothesis H3:

$$\mathbf{q}(a,t) = \begin{cases} R_\varepsilon(a,a-t)\mathbf{q}_0(a-t), & a>t, \\ R_\varepsilon(a,0)\mathbf{q}(0,t-a), & a<t, \end{cases}$$

where $\mathbf{q}(0,t)$ satisfies the following integral equation:

$$\begin{aligned} \mathbf{q}(0,t) &= \int_0^{+\infty} \mathbf{B}_S(a)\mathbf{q}(a,t)\,da \\ &= \int_0^t \mathbf{B}_S(a)R_\varepsilon(a,0)\mathbf{q}(0,t-a)\,da + \int_t^{+\infty} \mathbf{B}_S(a)R_\varepsilon(a,a-t)\mathbf{q}_0(a-t)\,da. \end{aligned} \tag{6.1}$$

Observe that

$$\|\mathcal{U}_\varepsilon(t)\mathbf{q}_0\|_{L^1(\mathbf{R}_+;\mathbf{R}^N)} = \int_0^t \|\mathbf{q}(a,t)\|\,da + \int_t^{+\infty} \|\mathbf{q}(a,t)\|\,da.$$

We compute both integrals in the above expression:

$$\int_t^{+\infty} \|\mathbf{q}(a,t)\,da = \int_t^{+\infty} \|R_\varepsilon(a,a-t)\mathbf{q}_0(a-t)\|\,da \leq C_2\|\mathbf{q}_0\|_{L^1} e^{(k_2-k_1/\varepsilon)t}, \tag{6.2}$$

$$\int_0^t \|\mathbf{q}(a,t)\|\,da \leq \int_0^t \|R_\varepsilon(a,0)\|\|\mathbf{q}(0,t-a)\|\,da \leq C_3\int_0^t e^{(k_2-k_1/\varepsilon)a}\|\mathbf{q}(0,t-a)\|\,da. \tag{6.3}$$

Bearing (6.1) in mind, we can write

$$\|\mathbf{q}(0,t)\| \leq C_4\int_0^t e^{(k_2-k_1/\varepsilon)a}\|\mathbf{q}(0,t-a)\|\,da + C_5\|\mathbf{q}_0\|_{L^1} e^{(k_2-k_1/\varepsilon)t}$$

from which it is easy to obtain $\|\mathbf{q}(0,t)\| \leq C_6\|\mathbf{q}_0\|_{L^1} e^{(C_7-k_1/\varepsilon)t}$. Substituting in (6.3) we have

$$\int_0^t \|\mathbf{q}(a,t)\|\,da \leq C_8\|\mathbf{q}_0\|e^{(C_7-k_1/\varepsilon)t}.$$

The lemma holds from this last inequality and (6.2), (6.3). ∎

Proof of Lemma 3.4. Remember that

$$(\mathcal{U}_\varepsilon(t)\mathbf{\Phi}_\varepsilon)(a) = \begin{cases} R_\varepsilon(a, a-t)\mathbf{\Phi}_\varepsilon(a-t) & (a > t), \\ R_\varepsilon(a, 0)Q(0, t-a) & (t > a), \end{cases}$$

where

$$Q(0,t) = \int_0^t \mathbf{B}_s(a)R_\varepsilon(a,0)Q(0,t-a)\,da + \int_t^{+\infty} \mathbf{B}_s(a)R_\varepsilon(a,a-t)\mathbf{\Phi}_\varepsilon(a-t)\,da.$$

(1) Estimation for $a > t$. Observe that $R_\varepsilon(a,\alpha) \circ R_\varepsilon(\alpha, b) = R_\varepsilon(a,b)$ and then

$$\begin{aligned}\left(\frac{\partial}{\partial\alpha}R_\varepsilon(a,\alpha)\right) \circ R_\varepsilon(\alpha,b) &= -R_\varepsilon(a,\alpha) \circ \left(\frac{\partial}{\partial\alpha}R_\varepsilon(\alpha,\beta)\right) \\ &= -R_\varepsilon(a,\alpha)\left[\frac{1}{\varepsilon}\mathbf{K}_S(\alpha) - \mathbf{M}_S(\alpha)\right]R_\varepsilon(\alpha,b)\end{aligned}$$

which implies

$$\left\|\frac{\partial}{\partial\alpha}R_\varepsilon(a,a-t)\right\| \le \frac{C_1}{\varepsilon}\|R_\varepsilon(a,a-t)\| \le \frac{C_1}{\varepsilon}e^{(k_2-k_1/\varepsilon)t}.$$

Conversely, from definition of $\mathbf{\Phi}_\varepsilon$ in Lemma 3.2, we can easily obtain the estimations

$$\|\mathbf{\Phi}_\varepsilon(a)\| \le C_2 e^{(k_2-k_1/\varepsilon)a}; \quad \|\mathbf{\Phi'}_\varepsilon(a)\| \le \frac{C_2}{\varepsilon}e^{(k_2-k_1/\varepsilon)a}.$$

Bearing in mind that

$$\left(\frac{d\mathcal{U}_\varepsilon}{dt}(t)\mathbf{\Phi}_\varepsilon\right)(a) = -\frac{\partial}{\partial\alpha}R_\varepsilon(a,a-t)\mathbf{\Phi}_\varepsilon(a-t) - R_\varepsilon(a,a-t)\mathbf{\Phi'}_\varepsilon(a-t),$$

the following estimation, valid for $a > t$, holds:

$$\left\|\left(\frac{d\mathcal{U}_\varepsilon}{dt}(t)\mathbf{\Phi}_\varepsilon\right)(a)\right\| \le \frac{C_3}{\varepsilon}e^{(k_2-k_1/\varepsilon)a}.$$

(2) Estimation for $a < t$. In this case,

$$\left(\frac{d\mathcal{U}_\varepsilon}{dt}\mathbf{\Phi}_\varepsilon\right)(a) = R_\varepsilon(a,0)\frac{\partial Q}{\partial t}(0,t-a).$$

Denoting $z(t) = Q(0,t)$, we have

$$\begin{aligned} z'(t) = \mathbf{B}_S(t)R_\varepsilon(t,0)z(0) &+ \int_0^t \mathbf{B}_S(a)R_\varepsilon(a,0)z'(t-a)\,da \\ -\mathbf{B}_S(t)R_\varepsilon(t,0)\mathbf{\Phi}_\varepsilon(0) &+ \int_t^{+\infty}\mathbf{B}_S(a)\frac{\partial}{\partial t}\left[R_\varepsilon(a,a-t)\mathbf{\Phi}_\varepsilon(a-t)\right]da.\end{aligned}$$

Since

$$\|z(0)\| \le C_4\int_0^{+\infty}\|\mathbf{\Phi}_\varepsilon(a)\|\,da \le C_4\int_0^{+\infty}e^{(k_2-k_1/\varepsilon)a}\,da \le C_4\varepsilon$$

and

$$\left\| \int_t^{+\infty} \mathbf{B}_S(a) \frac{\partial}{\partial t} \left[R_\varepsilon(a, a-t) \mathbf{\Phi}_\varepsilon(a-t) \right] da \right\| \leq \frac{C_5}{\varepsilon} \int_t^{+\infty} e^{(k_2 - k_1/\varepsilon)a} \, da = C_5 e^{(k_2 - k_1/\varepsilon)t},$$

standard calculations lead to

$$\|z'(t)\| \leq C_6 e^{(C_7 - k_1/\varepsilon)t}$$

from which we obtain the following estimation, valid for $t > a$:

$$\left\| \left(\frac{d\mathcal{U}_\varepsilon}{dt}(t) \mathbf{\Phi}_\varepsilon \right)(a) \right\| \leq C_8 e^{(C_9 - k_1/\varepsilon)t}.$$

We are now ready to obtain the estimate of the lemma:

$$\begin{aligned} \|\mathcal{V}_\varepsilon(t)(\cdot)\|_{L^1} &= \int_0^t \|\mathcal{V}_\varepsilon(t)(a)\| \, da + \int_t^{+\infty} \|\mathcal{V}_\varepsilon(t)(a)\| \, da \\ &\leq C_{10} t e^{(C_9 - k_1/\varepsilon)t} + C_{11} e^{(k_2 - k_1/\varepsilon)t} \leq C_{12} e^{(C_{13} - k_1/\varepsilon)t}. \qquad \square \end{aligned}$$

Proof of Lemma 3.5. We made only the calculations corresponding to the operator $\mathcal{D}_\varepsilon(t)$ since the calculations for the operator $\mathcal{B}_\varepsilon$ are similar.

$$\begin{aligned} \|\mathcal{D}_\varepsilon(t)p\|_{L^1(\mathbf{R}_+)} &\leq \int_0^{+\infty} \left| \mathbf{1}^T \mathbf{M}(a) \left(\int_0^t \mathcal{U}_\varepsilon(t-\tau) \left[\mathbf{M}_S(a) \boldsymbol{\nu}(a) + \boldsymbol{\nu}'(a) \right] p(a,\tau) \, d\tau \right) \right| da \\ &+ \int_0^{+\infty} \left| \mathbf{1}^T \mathbf{M}(a) \left(\int_0^t \mathcal{V}_\varepsilon(t-\tau)(a) \left(\int_0^{+\infty} p(\alpha,\tau) \mathbf{B}_S(\alpha) \boldsymbol{\nu}(\alpha) \, d\alpha \right) d\tau \right) \right| da \\ &\leq C_1 e^{(k_2 - k_1/\varepsilon)t} \int_0^{+\infty} \left(\int_0^t e^{-(k_2 - k_1/\varepsilon)\tau} |p(a,\tau)| \, d\tau \right) da \\ &+ C_2 \sup_{\tau \in [0,t]} \|p(\cdot,\tau)\|_{L^1} \int_0^t \left(\int_0^{+\infty} \|\mathcal{V}_\varepsilon(t-\tau)(a)\| \, da \right) d\tau \\ &\leq C_3 \varepsilon \sup_{\tau \in [0,\tau]} \|p(\cdot,\tau)\|_{L^1} \left[1 - e^{(C_4 - k_1/\varepsilon)t} \right] \leq \varepsilon C_3 \sup_{\tau \in [0,t]} \|p(\cdot,\tau)\|_{L^1}. \qquad \square \end{aligned}$$

Proof of Lemma 3.7. First of all, observe that

$$\begin{aligned} \|\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)(\cdot,t) - \mathcal{J}(0, p_0, \mathbf{0})(\cdot,t)\|_{L^1(\mathbf{R}_+)} &\leq \int_0^t \rho_0(a,0) |g_\varepsilon(t-a)| \, da \\ &+ \int_0^t \left(\int_0^a \rho_0(a,\sigma) |f_\varepsilon(\sigma, t-a+\sigma)| \, d\sigma \right) da \\ &+ \int_t^{+\infty} \left(\int_0^t \rho_0(a, a-t+\sigma) |f_\varepsilon(a-t+\sigma, \sigma)| \, d\sigma \right) da. \end{aligned}$$

The latter term is less than

$$C_1 \int_0^t \left(\int_t^{+\infty} e^{-\mu_*(t-\sigma)} e^{(C_2 - k_1/\varepsilon)\sigma} \|\mathbf{q}_0(a-t+\sigma)\| \, da \right) d\sigma \leq \varepsilon C_3 \|\mathbf{q}_0\|_{L^1} e^{-\mu_* t}$$

and the other two are estimated by

$$\begin{aligned} &C_4 \int_0^t e^{-\mu_* a} e^{(k_4 - k_1/\varepsilon)(t-a)} \|\mathbf{q}_0\|_{L^1} \, da + C_5 \int_0^t \left(\int_0^a \rho_0(a, a-s) |f_\varepsilon(a-s, t-s)| \, ds \right) da \\ &\leq \varepsilon C_6 \|\mathbf{q}_0\| e^{-\mu_* t} (1+t). \end{aligned}$$

Finally, both estimations yield

$$\begin{aligned}\|\mathcal{J}(\varepsilon, p_0, \mathbf{q}_0)(\cdot,t) - \mathcal{J}(0, p_0, \mathbf{0})(\cdot,t)\|_{L^1(\mathbf{R}_+)} &\le \varepsilon C_7 \|\mathbf{q}_0\|_{L^1(\mathbf{R}_+)} e^{-\mu_* t}(1+t) \\ &\le \varepsilon C_8 e^{-\tilde{\mu} t}\|\mathbf{q}_0\|_{L^1(\mathbf{R}_+)},\end{aligned}$$

where $\tilde{\mu}$ is any number such that $\tilde{\mu} < \mu_*$ and C_8 is an estimate in terms of $\tilde{\mu}$. ∎

Proof of Lemma 4.1. The resolvent kernel $\rho_\varepsilon(a, \alpha)$ is the solution of the problem

$$\begin{cases} v'(a) &= -\mu^*(a)v(a) + \int_\alpha^a r_\varepsilon(a,\beta)v(\beta)d\beta, \\ v(\alpha) &= 1. \end{cases}$$

Its expression is

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

From inequality (4.6) we get

$$\left| \int_\beta^a e^{-\int_s^a \mu^*(u)du} r_\varepsilon(s,\beta)ds \right| \le \varepsilon C_1,$$

where $C_1 > 0$ is a constant, and hence

$$v(a) \le e^{-k_M(a-\alpha)} + \varepsilon C_1 \int_\alpha^a v(\beta)d\beta. \tag{6.4}$$

Using the notation $W(p) = \int_0^p v(s+\alpha)ds$, the last inequality reads

$$W'(p) - \varepsilon C_1 W(p) \le e^{-k_M p}.$$

Integrating we obtain

$$W(p) \le \frac{e^{\varepsilon C_1 p} - e^{-k_M p}}{k_M + \varepsilon C_1}.$$

The proof of the lemma is completed by substituting the last inequality in (6.4). ∎

Proof of Proposition 4.2. If we write

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

then f_ε verifies the integral equation

$$f_\varepsilon(a) = 1 + \int_0^a d\alpha \left[\int_0^\alpha r_\varepsilon(\alpha,\beta) e^{\int_\beta^\alpha \mu^*(s)ds} f_\varepsilon(\beta)d\beta \right]. \tag{6.5}$$

We will treat the existence of f_ε as a problem of inversion of an operator in a certain space. To this end, for each $\gamma > 0$, we consider the space

$$E_\gamma = \{ f \in C([0,+\infty[); |f(a)| \le C_1 e^{\gamma a},\ a \ge 0\}$$

which is a Banach space with the following norm:

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

For each $\varepsilon > 0$ we define the operator $K_\varepsilon : E_\gamma \longrightarrow E_\gamma$:

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

It is straightforward to prove that

$$\|K_\varepsilon f\|_\gamma \leq \varepsilon C_2 \|f\|_\gamma \left[\frac{1}{\gamma} + \frac{\varepsilon}{C_3} \right],$$

where C_2 and C_3 are positive constants, and then for a fixed γ there exists $\varepsilon_0(\gamma) > 0$ such that for every $\varepsilon \in]0, \varepsilon_0(\gamma)]$ it is verified that $\|K_\varepsilon\|_\gamma < 1$.

Equation (6.5) can be written in the form

$$[(I - K_\varepsilon) f_\varepsilon](a) = 1,$$

and the last inequality yields that, for $\varepsilon \in]0, \varepsilon_0(\gamma)]$, there exists a unique solution $f_\varepsilon \in E_\gamma$.

Now we can write

$$\sup_{a\geq 0} |\rho_\varepsilon(a,0) - \rho_0(a,0)| \leq \|K_\varepsilon f_\varepsilon\|_{\mu_*} \leq \varepsilon C_2 \left[\frac{1}{\mu_*} + \frac{\varepsilon}{C_3} \right] \|f_\varepsilon\|_{\mu_*} \longrightarrow 0 \quad (\varepsilon \to 0_+).$$

The last inequality completes the proof of the proposition. $\square$

Proof of Proposition 4.5. (a) Essential compactness. Solving the system (3.1), (3.2), through the characteristic lines of the operator $(\partial/\partial a) + (\partial/\partial t)$, we have, for $a > t$,

$$\begin{bmatrix} p_\varepsilon(a,t) \\ \mathbf{q}_\varepsilon(a,t) \end{bmatrix} = \mathcal{R}_\varepsilon(a, a-t) \begin{bmatrix} p_0(a-t) \\ \mathbf{q}_0(a-t) \end{bmatrix},$$

where $\mathcal{R}_\varepsilon(s,\sigma)$ is the fundamental matrix of the system

$$\begin{aligned} \frac{du}{ds} &= -\mu^*(s)u(s) - \mathbf{1}^T \mathbf{M}(a)\mathbf{v}(s), \\ \frac{d\mathbf{v}}{ds} &= -[\mathbf{M}_S(a)\boldsymbol{\nu}(a) + \boldsymbol{\nu}'(a)]u(s) + \left[\frac{1}{\varepsilon}\mathbf{K}_S(a) - \mathbf{M}_S(a) \right] \mathbf{v}(s). \end{aligned}$$

Standard calculations allow us to estimate the norm $\|\mathcal{R}_\varepsilon(s,\sigma)\|$ in terms of the fundamental matrix $R_\varepsilon(s,\sigma)$ defined in Hypothesis H3. To be more specific, the existence of $\tilde{\varepsilon}_0 > 0$ can be proved such that, for all $\delta > 0$ there exists $\xi(\delta) > 0$, which satisfies

$$\|\mathcal{R}_\varepsilon(s,\sigma)\| \leq \xi(\delta) e^{-(\mu_* - \delta)(s-\sigma)}, \quad s \geq \sigma,$$

for all $0 < \varepsilon < \tilde{\varepsilon}_0$.

Then,

$$\|(p_\varepsilon(\cdot,t), \mathbf{q}_\varepsilon(\cdot,t))\|_{L^1([t,+\infty)} \leq \xi(\delta) e^{-(\mu_*-\delta)t} \|(p_0, \mathbf{q}_0)\|_{L^1(\mathbf{R}_+)}.$$

Let us denote by $\mathbf{I}_{[t_0,t_1]}$ the restriction of a function $\mathbf{F}(\cdot,t)$ to the interval $[t_0,t_1]$. We can write

$$T_\varepsilon(t) = \mathbf{I}_{[0,t]} T_\varepsilon(t) + \mathbf{I}_{[t,+\infty)} T_\varepsilon(t).$$

The term $\mathbf{I}_{[0,t]}T_\varepsilon(t)$ is an operator with some compact iterate and, from the above considerations we have, for $0 < \varepsilon < \tilde{\varepsilon}_0$,

$$\alpha\left(T_\varepsilon(t)\right) \leq \xi(\delta) e^{-(\mu_* - \delta)t},$$

where, as usual, $\alpha(\cdot)$ is the measure of noncompactness (see [35]). Then, the α-growth bound of the perturbed semigroup satisfies

$$\forall \delta > 0, \quad \omega_e\left(T_\varepsilon(t)\right) \leq -(\mu_* - \delta),$$

that is, $\omega_e\left(T_\varepsilon(t)\right) \leq -\mu_*$, with $\omega_e(\cdot)$ being, as usual, the essential growth bound of the perturbed semigroup.

In Proposition 4.4 it is ensured that, for $0 < \varepsilon < \varepsilon_0$, the infinitesimal generator of the semigroup has a real eigenvalue λ_ε such that $\lambda > -\mu_*$. This implies that

$$\omega_0\left(T_\varepsilon(t)\right) \geq \lambda_\varepsilon > -\mu_* \geq \omega_e\left(T_\varepsilon(t)\right).$$

Then, we can conclude that the semigroup $\{T_\varepsilon(t)\}_{t\geq 0}$ is essentially compact for $0 < \varepsilon < \min(\varepsilon_0, \tilde{\varepsilon_0})$.

(b) Irreducibility. We start by proving that, under Hypothesis H4, if for some $a_0 > 0$ and some i_0 we have $n_{i_0}(a_0, 0) > 0$, then

$$\forall i = 1, \ldots, N, \quad \forall s > 0, \quad n_i(a_0 + s, s) > 0.$$

Let us denote by $[\mathbf{K}(a)]_{i\neq j}$ the matrix $\mathbf{K}(a) - \operatorname{diag}\{k_{ii}(a);\ i = 1, \ldots, N\}$ and by $[\mathbf{K}(a)]_{i=j}$ the matrix $\operatorname{diag}\{k_{ii}(a);\ i = 1, \ldots, N\}$. By continuity, we have the following estimation for a in some neighborhood of a_0:

$$[\mathbf{K}(a)]_{i\neq j} \geq \frac{1}{2}\left[\mathbf{K}(a_0)\right]_{i\neq j}.$$

Solving the PDE (2.1) along the characteristic line which starts at $(a_0, 0)$, it is easy to obtain, for $s > 0$ small enough,

$$\frac{dn}{ds} \geq \left[-\mathbf{M}(a_0 + s) + \frac{1}{\varepsilon}\left[\mathbf{K}(a_0 + s)\right]_{i=j}\right] n + \frac{1}{2\varepsilon}\left[\left[\mathbf{K}(a_0)\right]_{i\neq j}\right] n.$$

Consider the function $\tilde{n}(s) = e^{rs} n(s)$, with $r > 0$ big enough to have the estimation

$$\frac{d\tilde{n}}{ds}(s) \geq \left[\frac{r}{2} Id + \frac{1}{2\varepsilon}\left[\mathbf{K}(a_0)\right]_{i\neq j}\right] \tilde{n}(s).$$

This implies that

$$\tilde{n}(s) \geq e^{(l/2)s} e^{(1/2\varepsilon)s[\mathbf{K}(a_0)]_{i\neq j}} \tilde{n}(0).$$

From positivity and irreducibility of matrix $\mathbf{K}(a_0)$, we can conclude that $\tilde{n}(s) > 0$ for $s > 0$ small enough, and the same is true along the characteristic line.

Hypothesis H4 implies that, for $t > a_1 - a_0$ if $a_1 > a_0$, or as well for $t > 0$ if $a_1 < a_0$, there exists $i = i(t)$ such that $n_{i(t)}(0, t) > 0$. Then, we have

$$\forall i = 1, \ldots N, \quad \forall s > 0, \quad n_i(s, t + s) > 0, \quad t > \max(0, a_1 - a_0).$$

Let $T > 0$ be such that $T > \max(0, a_1 - a_0)$. We have proved that

$$\forall i = 1, \ldots, N, \quad 0 \leq s \leq T, \quad \forall \tau > T + \max(0, a_1 - a_0), \quad n_i(s, \tau) > 0.$$

That is, the semigroup is positive and irreducible. $\square$

REFERENCES

[1] O. Arino, *Some spectral properties for the asymptotic behavior of semigroups connected to population dynamics*, SIAM Rev., 34 (1992), pp. 445–476.
[2] O. Arino, M. L. Hbid, and R. Bravo de la Parra, *A mathematical model of growth of population of fish in the larval stage: Density-dependence effects*, Math. Biosci., 150 (1998), pp. 1–20.
[3] O. Arino and M. Kimmel, *Asymptotic analysis of a cell cycle model based on unequal division*, SIAM J. Appl. Math., 47 (1987), pp. 128–145.
[4] O. Arino, C. Koutsikopoulos, and A. Ramzi, *Elements of mathematical modeling of evolution in number of a sole population*, J. Biol. Systems, 4 (1996), pp. 445–458.
[5] O. Arino and P. Prouzet, *Modeling of the Larval Stage of the Anchovy of the Bay of Biscay, Estimation of the Rate of Recruitment in the Juvenile Stage*, Interim Progress Report, DG XIV, European Community project 96/048, 1997.
[6] P. Auger, *Dynamics and Thermodynamics in Hierarchically Organized Systems. Applications in Physics, Biology and Economics*, Pergamon Press, Oxford, 1989.
[7] P. Auger and E. Benoit, *A prey-predator model in a multipatch environment with different time scales*, J. Biol. Systems, 1 (1993), pp. 187–197.
[8] P. Auger and R. Roussarie, *Complex ecological models with simple dynamics: From individuals to populations*, Acta Biotheoretica, 42 (1994), pp. 111–136.
[9] P. Auger and J. C. Poggiale, *Emerging properties in population dynamics with different time scales*, J. Biol. Systems, 3 (1995), pp. 591–602.
[10] R. Bravo de la Parra, P. Auger, and E. Sánchez, *Aggregation methods in discrete models*, J. Biol. Systems, 3 (1995), pp. 603–612.
[11] R. Bravo de la Parra, E. Sánchez, and P. Auger, *Time scales in density dependent discrete models*, J. Biol. Systems, 5 (1997), pp. 111–129.
[12] R. Bravo de la Parra, E. Sánchez, and P. Auger, *Aggregation methods in population dynamics discrete models*, Math. Comput. Modelling, 27 (1998), pp. 23–39.
[13] J. Horwood, *The Bristol Channel sole (Solea solea (L.)): A fishery case study*, Adv. Marine Biology, 29 (1993), pp. 215–367.
[14] E. D. Houde, *Comparative growth, mortality and energetics of marine fish larvae: Temperature and implied latitudinal effects*, Fishery Bull., 87 (1989), pp. 471–496.
[15] J. Kevorkian and J. D. Cole, *Multiple Scale and Singular Perturbation Methods*, Appl. Math. Sci., 114, Springer Verlag, Berlin, 1996.
[16] R. Z. Khasminskii, G. Yin, and Q. Zhang, *Asymptotic expansions of singularly perturbed systems involving rapidly fluctuating Markov chains*, SIAM J. Appl. Math., 56 (1996), pp. 277–293.
[17] C. Koutsikopoulos, L. Fortier, and J. Gagne, *Cross-shelf dispersion of Dover sole (Solea solea) eggs and larvae in Biscay Bay recruitment to inshore nurseries*, J. of Plankton Research, 13 (1991), pp. 923–945.
[18] R. Lasker, ed., *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis Mordax*, N.O.A.A. Technical Report NMFS, 36, 1985.
[19] L. Motos, *Reproductive biology and fecundity of the Bay of Biscay anchovy (Engraulis encrasicholus)*, Scientia Marina, 60 (suppl. 2) (1996), pp. 195–207.
[20] L. Motos, J. Santiago, and A. Uriarte, *Assessment of Spawning Biomass of the Bay of Biscay Anchovy Population, Engraulis encrasicholus L., Using the Daily Egg Production Method*, Technical Report ICES CM 1991/H: 33, 1991.
[21] L. Motos, Personal communication, 1998.
[22] M. Mullin, *Webs and Scales: Physical and Ecological Processes in Marine Fish Recruitment*, Books in Recruitment Fishery Oceanography, University of Washington Press, Seattle, WA, 1993.
[23] R. Nagel, ed., *One-parameter Semigroups of Positive Operators*, Lecture Notes in Math. 1184, Springer-Verlag, Berlin, 1986.
[24] A. Okubo, *Diffusion and Ecological Problems: Mathematical Models*, Biomathematics 10, Springer-Verlag, Berlin, 1980.
[25] P. Pepin, *Effect of temperature and size on development, mortality and survival rates of the pelagic early life history stages of marine fish*, Canad. J. Fish. Aquat. Sci., 48 (1991), pp. 503–518.
[26] P. Ru, *Anchovy spawning in the Mira estuary (southwestern Portugal)*, Scientia Marina, 60 (Suppl. 2) (1996), pp. 141–153.
[27] E. Sánchez, O. Arino, and M. Kimmel, *Noncompact semigroups of operators generated by*

cell kinetics models, Differential Integral Equations, 4 (1991), pp. 1233–1249.

[28] E. Sánchez, R. Bravo de la Parra, and P. Auger, *Linear discrete models with different time scales*, Acta Biotheoretica, 43 (1995), pp. 465–479.

[29] E. Seneta, *Non-negative Matrices and Markov Chains*, Springer-Verlag, Berlin, 1981.

[30] *Special Issue on Perturbation Methods in Physical Mathematics*, SIAM J. Appl. Math., 55 (1995), pp. 277–575.

[31] P. Tett and A. Edwards, *Mixing and plankton: An interdisciplinary theme in oceanography*, Oceanogr. Mar. Biol. Ann. Rev., 22 (1984), pp. 99–123.

[32] A. Uriarte and L. Motos, *Sampling errors in anchovy egg abundance estimates using the PAIROVET net*, J. of Plankton Research, 20 (1998), pp. 1861–1888.

[33] A. Uriarte, P. Prouzet, and B. Villamor, *Bay of Biscay and Ibero Atlantic anchovy populations and their fisheries*, Scientia Marina, 60 (Suppl. 2) (1996), pp. 237–255.

[34] W. J. Vlymen III, *Swimming energetics of the larval anchovy, Engraulis mordax*, Fishery Bull., 72 (1974), pp. 885–899.

[35] G. F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics*, Marcel Dekker, New York, 1985.