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Mathematical analysis of a population model with an age–weight structured two-stage life history: asymptotic behavior of solutions

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Abstract. In this paper, we propose a model for the dynamics of a physiologically structured population of individuals whose life cycle is divided into two stages: the first stage is structured by the weight, while the second one is structured by the age, the exit from the first stage occurring when a threshold weight is attained. The model originates in a complex one dealing with a fish population and covers a large class of situations encompassing two-stage life histories with a different structuring variable for each state, one of its key features being that the maturation process is determined in terms of a weight threshold to be reached by individuals in the first stage. Mathematically, the model is based on the classical Lotka–MacKendrick linear model, which is reduced to a delayed renewal equation including a constant delay that can be viewed as the time spent by individuals in the first stage to reach the weight threshold. The influence of the growth rate and the maturation threshold on the long-term behavior of solutions is analyzed using Laplace transform methods.

1. Introduction

The aim of this work was to propose and analyze a model for the dynamics of a physiologically structured population of individuals whose life cycle is divided into two stages with a different structure variable for each stage. The model originates in a complex one proposed in [4] which describes the growth of a population of fish. This model, trying to disentangle the massive regulation mechanisms of the abundance of many fish populations, describes in detail the population dynamics at the larval stage while the other stages of the life cycle are modeled using simple demographic mechanisms. The distinguishing feature of the model is that the exit from the larval stage is determined in terms of a weight threshold to be reached by the larvae. This kind of threshold models that can be transformed into state-dependent delayed equations are well represented in the literature, see [12,18] for general presentations and [2,6] for particular models in which the appearance of the delay is justified as a response of the maturation process to density dependence. In [4], a drastic simplification of the density-dependent model is suggested, yielding the whole dynamics to be reduced to a two-dimensional system of state-dependent delay equations.

The framework chosen for the model proposed in this paper is deliberately linear with the purpose of focusing readers' attention on the main mechanism: maturation represented by a larvae weight threshold. That is, we consider a general linear model of a population classified into two stages: larval and adult. The larval stage is structured by the weight, while the adult stage is structured by the age, the exit from the larval stage occurring when individuals reach a threshold weight. In this linear setting, the maturation threshold weight is assumed to be a priori given and hence not dependent on the population density.

This physiologically structured population model (PSPM) is based on the classical Lotka–MacKendrick linear model [8,9,14], which integrating along the characteristic lines can be reduced in a standard way to the so-called renewal equation for the function of births [7,13,14].

Keywords: Two-stage structured population, delayed renewal equation, Laplace transform, maturation threshold.

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This reduction process applied to PSPM with several stages leads to a linear delayed integral equation for the density of larvae at the maturation weight in which two different delays can be distinguished: the first one, τ^*, corresponding to the time spent by larvae in the larval stage and the second one, a^*, the maximum age attained by adults. Our assumptions on larvae growth and mortality rates, that are taken to be just weight dependent, make τ^* an individual feature in a constant environment and thus itself constant.

From a mathematical point of view, the main results established in this work concern the asymptotic behavior of solutions to the linear renewal equation which describes the evolution of the density of larvae at the maturation time. The linear formulation of the model allows Laplace transform methods to be used, but the occurrence of delays in the equation and the usual choice of L^1 as a suitable state space for initial data introduce some complex technical difficulties that prevent a direct application of standard theoretical results as described in [13].

Although we use in our model the terms larvae and adults to refer to the population stages, which is due to the origins of this work, it is clear that the abstract setting of the proposed system of partial differential equations encompasses the general class of threshold structured population models which incorporate a two-stage life history with stages usually called juvenile and adult and that are frequently found in the literature, see for instance [1,10,11,16]. A feature of the proposed model which usually is not treated in the literature has to do with the two stages being structured by two different state variables, juveniles by weight, or in general by size, and adults by age.

The organization of the paper is as follows. Section 2 presents the general model to be considered throughout together with its reduction to a delayed renewal equation in Sect. 2.1. Section 3 deals with the study of the asymptotic behavior of solutions via Laplace transform methods: asynchronous distributions of larvae and adults and an extinction condition are established. The paper ends with Sect. 4 by discussing the influence of larvae growth rate and the maturation threshold on the long-term behavior of the population.

2. Presentation of the model

Our work is concerned with the dynamics of a population classified into two stages: larvae (L) and adults (A). Individuals in stage (L) are characterized by their body weight w and are described by the density function $l(w,t)$ so that $\int_{w_1}^{w_2} l(w,t)\mathrm{d}w$ is the number of larvae in the population between weights w_1 and w_2 at time t. Adults (A) are structured by their chronological age a in the stage; the dynamics being described by the density function $n(a,t)$. Thus, $\int_{a_1}^{a_2} n(a,t)\mathrm{d}a$ is the number of adults in the population whose age belongs to the interval $[a_1,a_2]$ at time t. Since we are not considering spatial effects here, we assume that the population has a uniform distribution with respect to space and we normalize the number of individuals of every stage to the number per unit of volume.

Taking as a basis the classical Lotka–MacKendrick linear model of population dynamics, the density functions satisfy the model:

$$(\mathrm{A}) \quad \begin{cases} \dfrac{\partial n}{\partial t}(a,t) + \dfrac{\partial n}{\partial a}(a,t) = -\mu(a)n(a,t), \quad 0 < a < a^*,\ t > 0 & (\mathrm{A1}) \\ n(0,t) = g(w^*)l(w^*,t), \quad t > 0 & (\mathrm{A2}) \\ n(a,0) = n_0(a), \quad 0 < a < a^* & (\mathrm{A3}) \end{cases}$$

$$(\mathrm{L}) \quad \begin{cases} \dfrac{\partial l}{\partial t}(w,t) + \dfrac{\partial}{\partial w}[g(w)l(w,t)] = -\nu(w)l(w,t), \quad w_0 < w < w^*, \\ \hfill t > 0 \quad (\mathrm{L1}) \\ g(w_0)l(w_0,t) = \displaystyle\int_0^{a^*} \beta(a)n(a,t)\,\mathrm{d}a, \quad t > 0 \hfill (\mathrm{L2}) \\ l(w,0) = l_0(w), \quad w_0 < w < w^* \hfill (\mathrm{L3}) \end{cases}$$

where $\beta(a)$ and $\mu(a)$ are the age-dependent adult fertility and mortality rates, $\nu(w)$ and $g(w)$ are the weight-dependent larvae mortality and growth rates, and $n_0(a)$ and $l_0(w)$ are the initial adult age and larvae weight distributions.

We assume a maximum finite age $a^* > 0$ for adults and that vital rates β and μ are nonnegative functions satisfying:

$$\beta \in L^{\infty}(0, a^*), \quad \mu \in L^1_{\text{loc}}(0, a^*), \quad \int_0^{a^*} \mu(s)\, \mathrm{d}s = +\infty.$$

Larvae are assumed to be born with weight w_0 and mature on reaching weight w^*, $0 < w_0 < w^*$. Vital rates g and ν are positive functions that fulfill the following assumptions:

$$g \in C^1[w_0, w^*], \quad \nu \in L^1_{\text{loc}}(w_0, w^*).$$

We also assume that the initial data are nonnegative functions such that

$$n_0 \in L^1(0, a^*), \quad l_0 \in L^1(w_0, w^*).$$

Partial differential equations (A1) and (L1) correspond to the balance equations of, respectively, the classical McKendrick and continuous size-structured models [7,8,14]. Boundary condition (A2) represents the recruitment to stage (A), and it is the result of the maturation of larvae when reaching the maximum weight w^*. Boundary condition (L2) describes recruitment to stage (L) in terms of adult fertility. Equations (A3) and (L3) are the initial conditions. For the sake of completeness, we include a short justification of the boundary conditions (A2) and (L2) from a biological point of view, which follows closely some arguments explained in [15].

Let $S(t)$ be the rate of recruitment of larvae at birth at time t, so that during an infinitesimal time interval $[t, t + \mathrm{d}t]$, the total recruitment of larvae is $S(t)\mathrm{d}t$. The weights of these individuals belong to the interval $[w_0, w_0 + \mathrm{d}w_0]$, with $\mathrm{d}w_0 = g(w_0)\mathrm{d}t$ (the maximum possible gain of weight during $\mathrm{d}t$), and since the total number of larvae with weight in this range is $l(w_0, t)\mathrm{d}w_0$, we have:

$$S(t)\mathrm{d}t = l(w_0, t)\mathrm{d}w_0 = l(w_0, t)g(w_0)\mathrm{d}t.$$

On the other hand, bearing in mind that $S(t)$ is related with the fecundity of adults by $S(t) = \int_0^{a^*} \beta(a)n(a, t)\, \mathrm{d}a$, boundary condition (L2) follows. Condition (A2) can be justified by a similar argument, using the fact that the recruitment of larvae at the maximum weight w^* is related with $n(0, t)$.

As a first step toward the analytical study of system (A)–(L), we proceed to a standard integration of system (A) along the characteristic lines which allows adult density to be expressed in terms of larvae density:

(i) For $t \in [0, a^*]$:

$$n(a, t) = \begin{cases} n_0(a - t)e^{-\int_{a-t}^{a} \mu(s)\, \mathrm{d}s} & \text{if } t < a \\ g(w^*)l(w^*, t - a)e^{-\int_0^a \mu(s)\, \mathrm{d}s} & \text{if } t > a \end{cases}$$

(ii) For $t > a^*$:

$$n(a, t) = g(w^*)l(w^*, t - a)e^{-\int_0^a \mu(s)\, \mathrm{d}s}.$$

In turn, these values of $n(a, t)$ can be substituted into Eq. (L2), reducing the (A)–(L) system to the following one for the density of larvae:

$$\frac{\partial l}{\partial t}(w, t) + g(w)\frac{\partial l}{\partial w}(w, t) = -\delta(w)l(w, t), \; w_0 < w < w^*, \; t > 0 \tag{1}$$

$$l(w_0, t) = \begin{cases} G(t; n_0) + \displaystyle\int_0^t \Pi(a)l(w^*, t - a)\, \mathrm{d}a & \text{if } 0 < t < a^* \\ \displaystyle\int_0^{a^*} \Pi(a)l(w^*, t - a)\, \mathrm{d}a & \text{if } t > a^* \end{cases} \tag{2}$$

$$l(w, 0) = l_0(w), \; w_0 < w < w^* \tag{3}$$

where we have introduced the notations:

$$\delta(w) := \nu(w) + g'(w); \quad \Pi(a) := \frac{g(w^*)}{g(w_0)}\beta(a)e^{-\int_0^a \mu(s)\, \mathrm{d}s}$$

$$G(t; n_0) := \int_t^{a^*} \frac{1}{g(w_0)}\beta(a)e^{-\int_{a-t}^{a} \mu(s)\, \mathrm{d}s} n_0(a - t)\, \mathrm{d}a.$$

2.1. Reduction of the model (1)–(2)–(3) to a delayed renewal equation

First of all, we integrate this model along the characteristic lines, which are defined by the growth law:

$$\frac{\mathrm{d}w}{\mathrm{d}t} = g(w).$$

The characteristic line passing through $(w_0, 0)$ is:

$$t = \tau(w), \quad \tau(w) := \int_{w_0}^{w} \frac{\mathrm{d}s}{g(s)}$$

which can be interpreted as the time employed by an individual born with the minimum weight $w_0 > 0$ to reach a weight $w > w_0$. We will assume that individuals reach the maximum weight in a finite time, that is:

HYPOTHESIS 1.

$$\tau^* := \int_{w_0}^{w^*} \frac{\mathrm{d}s}{g(s)} < +\infty.$$

Then, a standard calculation leads to:

$$l(w,t) = \begin{cases} l_0(\tau^{-1}(\tau(w)-t))\dfrac{E(\tau(w))}{E(\tau(w)-t)} & \text{if } 0 < t < \tau(w) \\ l(w_0, t-\tau(w))E(\tau(w)) & \text{if } t > \tau(w) \end{cases} \tag{4}$$

where $E(u) := e^{-\int_0^u \delta(\tau^{-1}(s))\,\mathrm{d}s}$.

Since Eq. (2) provides a relationship between $l(w_0, t)$ and $l(w^*, t)$, expression (4) allows us to reduce the problem to a delayed linear integral equation in the state variable $R(t) := l(w^*, t)$, the density of larvae at the maturation threshold. Expression (4) leads to, for $t > \tau^*$:

$$l(w^*, t) = l(w_0, t-\tau^*)E(\tau^*)$$

so that, Eq. (2) provides:

(i) For $t \in [\tau^*, \tau^* + a^*]$:

$$R(t) = E(\tau^*)G(t-\tau^*; n_0) + E(\tau^*)\int_0^{t-\tau^*} \Pi(a)R(t-\tau^*-a)\,\mathrm{d}a$$

(ii) For $t > \tau^* + a^*$:

$$R(t) = E(\tau^*)\int_0^{a^*} \Pi(a)R(t-\tau^*-a)\,\mathrm{d}a.$$

Introducing the notations:

$$\Pi^*(a) := E(\tau^*)\Pi(a); \quad N_0(t) := E(\tau^*)G(t; n_0), \quad a, t \in [0, a^*]$$
$$L_0(t) := l_0(\tau^{-1}(\tau^* - t))\frac{E(\tau^*)}{E(\tau^*-t)}, \quad t \in [0, \tau^*]$$

we have obtained for $R(t)$ the following functional equation:

$$R(t) = \begin{cases} L_0(t) & \text{if } t \in [0, \tau^*] \\ N_0(t-\tau^*) + \displaystyle\int_0^{t-\tau^*} \Pi^*(a)R(t-\tau^*-a)\,\mathrm{d}a & \text{if } t \in [\tau^*, \tau^*+a^*] \\ \displaystyle\int_0^{a^*} \Pi^*(a)R(t-\tau^*-a)\,\mathrm{d}a & \text{if } t > \tau^* + a^* \end{cases} \tag{5}$$

Straightforward calculations lead to

$$\Pi^*(a) = \beta(a)e^{-\int_0^a \mu(s)\mathrm{d}s}e^{-\int_{w_0}^{w^*}(\nu(w)/g(w))\mathrm{d}w} \tag{6}$$

The term $e^{-\int_{w_0}^{w^*}(\nu(w)/g(w))\mathrm{d}w}$ represents the probability that a larva survives and reaches the maturation weight w^* [8]. The probability for an adult to survive to age a corresponds to the term $e^{-\int_0^a \mu(s)\mathrm{d}s}$, that together with the adult fertility $\beta(a)$ give the so-called *maternity function* [13] for age-structured models. Let us define the parameter called *net reproduction rate* for model (A)–(L):

$$\Gamma_0 := \int_0^{a^*} \Pi^*(a)\mathrm{d}a = e^{-\int_{w_0}^{w^*}(\nu(w)/g(w))\mathrm{d}w} \cdot \int_0^{a^*} \beta(a)e^{-\int_0^a \mu(s)\mathrm{d}s}\mathrm{d}a \tag{7}$$

which gives the expected number of offspring produced by one individual during her reproductive life considering together both stages (A) and (L). We will see in the next section that the population either grows or declines exponentially depending on the values of parameter Γ_0.

A standard step-by-step procedure applied to expression (5) in intervals $[k\tau^*, (k+1)\tau^*]$, $k = 0, 1, \ldots$ allows $R(t)$ to be constructed in $\mathbf{R}_+$. Notice that extending by zero to $\mathbf{R}$ the definitions of the initial data n_0, l_0 and the rates β, μ, Eq. (5) can be written as:

$$R(t) = \tilde{L}_0(t) + \tilde{N}_0(t-\tau^*) + \int_0^{t-\tau^*} \tilde{\Pi}^*(a)R(t-\tau^*-a)\,\mathrm{d}a, \quad t \geq 0$$

where we have introduced the notations $\tilde{L}_0$, $\tilde{N}_0$, and $\tilde{\Pi}^*$ to represent the extension by zero to $\mathbf{R}$ of the functions L_0, N_0, and Π^*, respectively.

Applying well-known general theoretical results on continuity of translations in $L^1(\mathbf{R})$, it is easy to check the continuity of the functions defined by:

$$\forall\, t \in \mathbf{R}, \quad t \to \int_t^{a^*} K(a)f(t-a)\,\mathrm{d}a, \quad t \to \int_0^t K(a)f(t-a)\,\mathrm{d}a$$

where $K \in L^\infty(\mathbf{R})$, $f \in L^1(\mathbf{R})$, from which the continuity of functions $t \to \tilde{N}_0(t)$ and $t \to \int_0^t \tilde{\Pi}^*(a)R(t-a)\,\mathrm{d}a$ for $t \geq 0$ can be immediately deduced.

As an immediate consequence, we have:

THEOREM 1. *For each initial data $n_0 \in L^1(0, a^*)$, $l_0 \in L^1(w_0, w^*)$, there exists a unique solution $R(t)$ to (5), which is defined for $t \geq 0$ and $R \in L^1_{\mathrm{loc}}(\mathbf{R}_+)$. This solution satisfies that $R(t) \geq 0$ for $t \geq 0$ if both initial data n_0, l_0 are nonnegative. Moreover, $R(t)$ is continuous for $t \geq \tau^*$.*

Notice that the model (A)–(L) is being analyzed through Eq. (5). Therefore, Theorem 1 provides existence, uniqueness, and positivity of solutions to (A)–(L) corresponding to nonnegative initial data n_0, l_0.

3. Asymptotic behavior of solutions

In this section, we will establish the asymptotic behavior of solutions to (5) by applying Laplace transform methods (see [13]). To this end and bearing in mind that $R \in L^1_{\mathrm{loc}}(\mathbf{R})$, we start by showing that the solutions $R(t)$ to (5) are exponentially bounded for t big enough, so that their Laplace transform exist.

Let $R_{k+1}(t)$ be the restriction of $R(t)$ to the interval $[k\tau^*, (k+1)\tau^*]$. Set $k_0 \geq 2(\tau^* + a^*)/\tau^*$. Then, for $k \geq k_0$, $t \in [k\tau^*, (k+1)\tau^*]$ implies that $t \geq \tau^* + a^*$, so that R_{k+1} is continuous and satisfies:

$$\begin{aligned}
\|R_{k+1}\|_\infty &:= \sup_{t\in[k\tau^*,(k+1)\tau^*]} |R_{k+1}(t)| \\
&= \sup_{t\in[k\tau^*,(k+1)\tau^*]} \left| \int_0^{a^*} \Pi^*(a)R(t-\tau^*-a)\,\mathrm{d}a \right| \\
&\leq \|\Pi^*\|_{L^1(0,a^*)} \left(\sup_{t\in[(k-1)\tau^*-a^*,k\tau^*]} |R(t)| \right).
\end{aligned}$$

Choosing some constant $M > \max(1, \|\Pi^*\|_{L^1(0,a^*)})$, a straightforward calculation leads to:

$$\|R_{k_0+p}\|_\infty \leq \|\Pi^*\|_{L^1(0,a^*)} \max\left(R_0^*, \|R_{k_0+1}\|_\infty, , \ldots, \|R_{k_0+(p-1)}\|_\infty\right) \leq M^p R_0^*$$

$p = 1, 2, \ldots$ where $R_0^* := \sup_{t\in[(k_0-1)\tau^*-a^*, k_0\tau^*]} |R(t)|$.

Since $(k_0+p)\tau^* \leq t \leq (k_0+p+1)\tau^*$ implies that $p \leq t/\tau^* - k_0$, we have for all $t \geq k_0\tau^* \geq 2(\tau^*+a^*)$:

$$|R(t)| \leq R_0^* M^{t/\tau^*-k_0} = M^{-k_0} R_0^* e^{(\log M/\tau^*)t}$$

as we wanted to prove.

Now, set $\hat{R}(p)$, $p \in \mathbf{C}$, to denote the Laplace transform of $R(t)$, solution to (5). We have:

$$\begin{aligned}\hat{R}(p) &= \int_0^{\tau^*} e^{-pt} L_0(t)\,\mathrm{d}t + \int_{\tau^*}^{\tau^*+a^*} e^{-pt} N_0(t-\tau^*)\,\mathrm{d}t \\ &\quad + \int_{\tau^*}^{+\infty} e^{-pt}\left(\int_0^{t-\tau^*} \tilde{\Pi}^*(a) R(t-\tau^*-a)\,\mathrm{d}a\right)\mathrm{d}t \\ &= \hat{L}_0(p) + e^{-p\tau^*}\hat{N}_0(p) + e^{-p\tau^*}\int_0^{+\infty} e^{-pt}(\tilde{\Pi}^* * R)(t)\,\mathrm{d}t \\ &= \hat{L}_0(p) + e^{-p\tau^*}\hat{N}_0(p) + e^{-p\tau^*}\hat{\Pi}(p)\hat{R}(p)\end{aligned}$$

where $\hat{L}_0(p)$, $\hat{N}_0(p)$, and $\hat{\Pi}(p)$ are, respectively, the Laplace transforms of the functions $\tilde{L}_0(t)$, $\tilde{N}_0(t)$, and $\tilde{\Pi}^*(a)$.

Setting $\hat{H}(p) := \hat{L}_0(p) + e^{-p\tau^*}\hat{N}_0(p)$ (which is an entire function), we obtain the following expression for the Laplace transform of the solution:

$$\hat{R}(p) = \frac{\hat{H}(p)}{1 - e^{-p\tau^*}\hat{\Pi}(p)} = \hat{H}(p) + \frac{e^{-p\tau^*}\hat{H}(p)\hat{\Pi}(p)}{1 - e^{-p\tau^*}\hat{\Pi}(p)}, \quad \mathrm{Re}\, p > b^* \ \text{(abscissa of convergence)} \tag{8}$$

Notice that $\hat{H}(p)$ is the Laplace transform of $H(t) := \tilde{L}_0(t) + \tilde{N}_0(t-\tau^*)$, $t \geq 0$. Therefore, we can obtain the asymptotic behavior of $R(t)$ using the Laplace transform inversion formula, from the analysis of the function $F(t)$ defined by:

$$F(t) := \frac{1}{2\pi i} \lim_{T\to+\infty} \int_{b-iT}^{b+iT} e^{pt}\hat{F}(p)\,\mathrm{d}p \quad (b > b^*); \quad \hat{F}(p) := \frac{e^{-p\tau^*}\hat{\Pi}(p)\hat{H}(p)}{1 - e^{-p\tau^*}\hat{\Pi}(p)}. \tag{9}$$

A first step to calculate the above integral consists of locating the singularities of $\hat{F}(p)$, which are poles that must be found among the roots of the transcendental equation:

$$1 - e^{-p\tau^*}\hat{\Pi}(p) = 0. \tag{10}$$

With respect to this equation, we have:

PROPOSITION 1. *Equation (10) has one and only one real solution α^* which is a simple root. Any other solution p^* to (10) is such that Re $p^* < \alpha^*$ and within any strip of the complex plane $-\infty < b_1 \leq$ Re $p \leq b_2 < +\infty$ there is at most a finite number of roots.*

Moreover, $\alpha^* < 0$ if and only if $\Gamma_0 < 1$, where Γ_0 has been defined in (7).

Proof. Let us consider the function $\psi : \mathbf{R} \longrightarrow \mathbf{R}$ defined by:

$$\forall\,\lambda \in \mathbf{R}, \quad \psi(\lambda) := e^{-\lambda\tau^*}\hat{\Pi}(\lambda) = \int_0^{a^*} e^{-\lambda(a+\tau^*)}\Pi^*(a)\,\mathrm{d}a.$$

It is a C^1 strictly decreasing function such that $\lim_{\lambda\to-\infty}\psi(\lambda) = +\infty$ and $\lim_{\lambda\to+\infty}\psi(\lambda) = 0$. Therefore, there exists one and only one real value α^* such that $\psi(\alpha^*) = 1$, which is the unique real solution to Eq. (10) and which is a simple root since $\forall\,\lambda \in \mathbf{R}$, $\psi'(\lambda) < 0$. Moreover, it is evident that $\alpha^* < 0$ if and only if $\psi(0) < 1$.

On the other hand, set $p^* = \alpha + i\beta$ $(\beta \neq 0)$ a complex solution to (10). Then, we have

$$\begin{aligned}\psi(\alpha) &= \int_0^{a^*} e^{-\alpha(a+\tau^*)}\Pi^*(a)\,\mathrm{d}a \\ &> \int_0^{a^*} e^{-\alpha(a+\tau^*)}\cos\beta(\tau^*+a)\Pi^*(a)\,\mathrm{d}a = 1 = \psi(\alpha^*)\end{aligned}$$

which implies that $\alpha < \alpha^*$, that is, α^* is a strictly dominant real part root of (10).

Finally, let us examine the roots of (10) within a strip of the complex plane $-\infty < b_1 \leq \mathrm{Re}\, p \leq b_2 < +\infty$. As these roots are the zeros of an entire function, they constitute at most a sequence $\{p_n\}_{n=1,2,\ldots}$ without accumulation points, which in the case of being an infinite sequence, implies that $\lim_{n\to\infty} |\mathrm{Im}\, p_n| = +\infty$. Since $\{\mathrm{Re}\, p_n\}_{n=1,2,\ldots}$ is a bounded set, the Riemann–Lebesgue lemma implies that $\lim_{n\to\infty} \int_0^{a^*} e^{-p_n(a+\tau^*)}\Pi^*(a)\,\mathrm{d}a = 0$, which contradicts the fact that each p_n is a root of (10).

This finishes the proof of the proposition. ☐

To estimate the integral appearing in (9), we will apply the residue theorem to a positively oriented circuit Γ constituted by a rectangle defined by the points $b_0 \pm iT$, $b_1 \pm iT$ $(T > 0)$ such that $b_1 < \alpha^* < b_0$ and all the other complex roots p^* to Eq. (10) satisfy that $\mathrm{Re}\, p^* < b_1$. There is no loss of generality choosing $b_0 > 0$.

An immediate consequence of Proposition 1 is that α^* is a simple pole of this integral, so that:

$$\int_\Gamma e^{pt}\hat{F}(p)\,\mathrm{d}p = 2\pi i \mathrm{Res}\,(\alpha^*) \tag{11}$$

where

$$\mathrm{Res}(\alpha^*) = \lim_{p\to\alpha^*}(p-\alpha^*)e^{pt}\hat{F}(p) = C^*(l_0, n_0)e^{\alpha^*(t-\tau^*)}$$

and

$$C^*(l_0, n_0) := \frac{\hat{\Pi}(\alpha^*)\hat{H}(\alpha^*)}{\int_0^{a^*}(\tau^*+a)e^{-\alpha^*(\tau^*+a)}\Pi^*(a)\,\mathrm{d}a}. \tag{12}$$

Let us obtain an estimation for this constant. In what follows we simplify by denoting C_i, $i = 1, 2, \ldots$ all the positive constants that appear in calculations and whose specific values are not relevant for our purposes.

Since:

(i) For $t \in [0, \tau^*]$:

$$|L_0(t)| \leq \left|\frac{E(\tau^*)}{E(\tau^*-t)}\right| |l_0(\tau^{-1}(\tau^*-t))| \leq |l_0(\tau^{-1}(\tau^*-t))|$$

(ii) For $u \in [0, a^*]$:

$$|N_0(u)| \leq |E(\tau^*)||G(u; n_0)| \leq \frac{\|\beta\|_\infty}{g(w_0)}\int_u^{a^*}|n_0(a-u)|\mathrm{d}a \leq \frac{\|\beta\|_\infty}{g(w_0)}\|n_0\|_{L^1(0,a^*)}$$

we have:

$$\begin{aligned}|\hat{H}(\alpha^*)| &\leq \int_0^{\tau^*} e^{-\alpha^* t}|L_0(t)|\,\mathrm{d}t + e^{-\alpha^*\tau^*}\int_0^{a^*} e^{-\alpha^* u}|N_0(u)|\,du \\ &\leq C_1[\|l_0\|_{L^1(w_0,w^*)} + \|n_0\|_{L^1(0,a^*)}]\end{aligned}$$

which immediately provides:

$$|C^*(l_0, n_0)| \leq M^*[\|l_0\|_{L^1(w_0,w^*)} + \|n_0\|_{L^1(0,a^*)}]$$

for some constant $M^* > 0$, depending on α^*, τ^*.

Retaking the calculation of the integral in the left-hand side of (11), notice that the two terms corresponding to the horizontal sides of Γ in this complex integral are:

$$\int_{b_1}^{b_0} e^{(\sigma-iT)t}\,\hat{F}(\sigma-iT)\,\mathrm{d}\sigma-\int_{b_1}^{b_0} e^{(\sigma+iT)t}\,\hat{F}(\sigma+iT)\,\mathrm{d}\sigma=-2i\,\mathrm{Im}\,J(T,t)$$

where

$$J(T,t):=\int_{b_1}^{b_0} e^{(\sigma+iT)t}\,\hat{F}(\sigma+iT)\,\mathrm{d}\sigma.$$

LEMMA 1. *For each* $t\geq 0$, *we have* $\lim_{T\to+\infty} J(T,t)=0$.

Proof. Set

$$g(x+iy):=1-e^{-(x+iy)\tau^*}\hat{\Pi}(x+iy)=1-\int_0^{a^*} e^{-(x+iy)(\tau^*+a)}\Pi^*(a)\,\mathrm{d}a. \tag{13}$$

Then, for $b_1\leq\sigma_1<\sigma_2\leq b_0$, we have:

$$\begin{aligned}|g(\sigma_2+iT)-g(\sigma_1+iT)| &\leq \int_0^{a^*}\Pi^*(a)|e^{-\sigma_1(\tau^*+a)}-e^{-\sigma_2(\tau^*+a)}|\,\mathrm{d}a\\ &\leq |\sigma_1-\sigma_2|\int_0^{a^*}\Pi^*(a)(\tau^*+a)\sup_{\sigma\in[b_1,b_0]}|e^{-\sigma(\tau^*+a)}|\,\mathrm{d}a\\ &:= C_1|\sigma_2-\sigma_1|.\end{aligned}$$

We claim that there exists a constant $g_0>0$ such that for any $T_0>0$ we have:

$$\inf_{(\sigma,T)\in[b_1,b_0]\times[T_0,+\infty)}|g(\sigma+iT)|\geq g_0.$$

If this is not true, then there exists a sequence $\{(\sigma_n,T_n)\}_{n=1,2,\ldots}\subset[b_1,b_0]\times[T_0,\infty)$ such that $\lim_{n\to\infty} g(\sigma_n+iT_n)=0$. It is simple to argue that there is no loss of generality assuming that $\lim_{n\to\infty}\sigma_n=\sigma^*\in[b_1,b_0]$ and also that $\lim_{n\to\infty}T_n=+\infty$.

Since the Riemann–Lebesgue lemma yields to $\lim_{T\to+\infty} g(\sigma+iT)=1$ for each $\sigma\in[b_1,b_0]$, we have:

$$\begin{aligned}|g(\sigma_n+iT_n)-1| &\leq |g(\sigma_n+iT_n)-g(\sigma^*+iT_n)|+|g(\sigma^*+iT_n)-1|\\ &\leq C_1|\sigma_n-\sigma^*|+|g(\sigma^*+iT_n)-1|\longrightarrow 0\ (n\to\infty)\end{aligned}$$

which is a contradiction.

Therefore, we have for $T\geq T_0>0$ and $t\geq 0$:

$$\begin{aligned}|J(T,t)| &\leq \left|\int_{b_1}^{b_0} e^{(\sigma+iT)t}\frac{e^{-(\sigma+iT)\tau^*}\hat{\Pi}(\sigma+iT)\hat{H}(\sigma+iT)}{g(\sigma+iT)}\,\mathrm{d}\sigma\right|\\ &\leq \frac{e^{b_0|t-\tau^*|}}{g_0}\int_{b_1}^{b_0}|\hat{\Pi}(\sigma+iT)||\hat{H}(\sigma+iT)|\,\mathrm{d}\sigma\longrightarrow 0\ (T\to+\infty).\end{aligned}$$

In the last integral, we have applied the Lebesgue dominated convergence theorem, bearing in mind that the Riemann–Lebesgue lemma assures for each $\sigma\in[b_1,b_0]$ that

$$\lim_{T\to+\infty}\hat{\Pi}(\sigma+iT)=\lim_{T\to+\infty}\hat{H}(\sigma+iT)=0.$$

The lemma is proved. □

As a consequence, taking the limit when $T \to +\infty$ in (11), the inversion formula (9) provides:

$$F(t) = C^*(l_0, n_0)e^{\alpha^*(t-\tau^*)} + \frac{1}{2\pi i} \lim_{T\to+\infty} \int_{b_1-iT}^{b_1+iT} e^{pt} \hat{F}(p)\, \mathrm{d}p. \tag{14}$$

To obtain the asymptotic behavior of $R(t)$ when $t \to +\infty$, we have to estimate the dependence with respect to t of the improper complex integral in the right-hand side of (14).

First of all notice that:

$$\begin{aligned} \frac{1}{2\pi i} \int_{b_1-iT}^{b_1+iT} e^{pt} \hat{F}(p)\, \mathrm{d}p &= \frac{e^{b_1(t-\tau^*)}}{2\pi} \int_{-T}^{T} e^{i\sigma(t-\tau^*)} \frac{\hat{\Pi}(b_1+i\sigma)\hat{H}(b_1+i\sigma)}{g(b_1+i\sigma)}\, \mathrm{d}\sigma \\ &= \frac{e^{b_1(t-\tau^*)}}{2\pi} I(T, t) \end{aligned}$$

where we have introduced the notation:

$$I(T, t) := \int_{-T}^{T} e^{i\sigma(t-\tau^*)} \frac{\hat{H}(b_1+i\sigma)\hat{\Pi}(b_1+i\sigma)}{g(b_1+i\sigma)}\, \mathrm{d}\sigma.$$

The usual choice in population dynamics models of $L^1(w_0, w^*)$ as state space for the initial data l_0 introduces some technical difficulties in the behavior of the integral $I(T, t)$ for $T \to +\infty$, that can be solved by imposing additional regularity conditions to the vital rates β and μ. To be precise, we will assume the following:

HYPOTHESIS 2. *The extension by zero to* $\mathbf{R}$ *of the function* $a \to \Pi^*(a)$, $a \in [0, a^*]$ *belongs to* $C^2(\mathbf{R})$.

Then, we have:

LEMMA 2. *The improper integral* $I^*(t) := \lim_{T\to+\infty} I(T, t)$ *is absolutely convergent and bounded by a constant non-dependent on* $t > 0$.

Proof. Since the vertical line $\mathrm{Re}\, p = b_1$ does not contain any solution to (10), then $\sigma \to |g(b_1 + i\sigma)|$ is a strictly positive and continuous function such that $\lim_{\sigma\to\pm\infty} |g(b_1 + i\sigma)| = 1$. Therefore, $g_1 := \inf_{\sigma\in\mathbf{R}} |g(b_1 + i\sigma)|$ is a strictly positive constant so that:

$$|I(T, t)| \le \frac{1}{g_1} \int_{-T}^{T} |\hat{H}(b_1+i\sigma)||\hat{\Pi}(b_1+i\sigma)|\, \mathrm{d}\sigma. \tag{15}$$

Let us notice that $\hat{H}(b_1 + i\sigma)$ and $\hat{\Pi}(b_1 + i\sigma)$, $\sigma \in \mathbf{R}$, are, respectively, the Fourier transforms of the two functions $t \to e^{-b_1 t}\left[\tilde{L}_0(t) + \tilde{N}_0(t - \tau^*)\right]$ and $a \to e^{-b_1 a}\tilde{\Pi}^*(a)$.

The mathematical complexity mentioned above appears because the function $t \to \tilde{L}_0(t)$ belongs to $L^1(\mathbf{R})$, and therefore, we can also assure that its Fourier transform is a continuous and bounded function on $\mathbf{R}$, which in general does not belong to $L^2(\mathbf{R})$, making impossible to apply the Parseval–Plancherel identity to estimate the integral in (15).

It is a well-known fact that the Fourier transform $\mathcal{F}(f)$ of a function $f \in L^1(\mathbf{R})$ is a continuous function on $\mathbf{R}$ bounded by:

$$\|\mathcal{F}(f)\|_\infty := \sup_{\sigma\in\mathbf{R}} |\mathcal{F}(f)(\sigma)| \le \|f\|_{L^1(\mathbf{R})}$$

so that in our case, straightforward calculations provide:

$$\begin{aligned} \sup_{\sigma\in\mathbf{R}} |\hat{H}(b_1+i\sigma)| &\le \int_0^{\tau^*} e^{-b_1 t}|L_0(t)|\, \mathrm{d}t + \int_0^{a^*} e^{-b_1(s+\tau^*)}|N_0(s)|\, \mathrm{d}s \\ &\le C_1[\|l_0\|_{L^1(w_0,w^*)} + \|n_0\|_{L^1(0,a^*)}]. \end{aligned}$$

On the other hand, assuming Hypothesis 2, standard properties of the Fourier transform, that relate the order of differentiability of a function with the growth at infinity of its Fourier transform, provide that the function $\sigma \to \sigma^2 \hat{\Pi}(b_1 + i\sigma)$ belongs to $L^\infty(\mathbf{R})$, which immediately implies the convergence of the improper integral $\int_{-\infty}^{+\infty} |\hat{\Pi}(b_1 + i\sigma)| \, \mathrm{d}\sigma$.

Summing up, we obtain from (15):

$$\begin{aligned} |I(T,t)| &\leq \frac{1}{g_1} \sup_{\sigma \in \mathbf{R}} |\hat{H}(b_1 + i\sigma)| \int_{-T}^{T} |\hat{\Pi}(b_1 + i\sigma)| \, \mathrm{d}\sigma \\ &\leq \frac{C_1}{g_1} [\|l_0\|_{L^1(w_0, w^*)} + \|n_0\|_{L^1(0,a^*)}] \int_{-\infty}^{+\infty} |\hat{\Pi}(b_1 + i\sigma)| \, \mathrm{d}\sigma \end{aligned}$$

from which we obtain:

$$|I^*(t)| \leq \lim_{T \to +\infty} |I(T,t)| \leq C_2 [\|l_0\|_{L^1(w_0, w^*)} + \|n_0\|_{L^1(0,a^*)}] \tag{16}$$

and the lemma is proved. □

We can now establish the asymptotic behavior of $R(t)$ for $t \to +\infty$, which constitutes the main result of this section:

THEOREM 2. *For each initial data $l_0 \in L^1(w_0, w^*)$, $n_0 \in L^1(0, a^*)$, the solution to (5) can be written as:*

$$R(t) = e^{\alpha^*(t-\tau^*)}[C^*(l_0, n_0) + \Omega(t)], \quad t > 0$$

for some function $\Omega(t)$ such that $\lim_{t \to +\infty} \Omega(t) = 0$, where α^* is the unique real solution to (10), and the constant $C^*(l_0, n_0) \geq 0$ has been defined in (12).

Proof. The Laplace inversion formula applied to expression (8) together with (14) yields to:

$$\begin{aligned} R(t) &= H(t) + F(t) = \tilde{L}_0(t) + \tilde{N}_0(t - \tau^*) + F(t) \\ &= \tilde{L}_0(t) + \tilde{N}_0(t - \tau^*) + C^*(l_0, n_0) e^{\alpha^*(t-\tau^*)} + \frac{e^{b_1(t-\tau^*)}}{2\pi} I^*(t) \\ &= e^{\alpha^*(t-\tau^*)}[C^*(l_0, n_0) + \Omega(t)] \end{aligned}$$

with:

$$\Omega(t) := e^{-\alpha^*(t-\tau^*)}[\tilde{L}_0(t) + \tilde{N}_0(t - \tau^*)] + \frac{e^{(b_1 - \alpha^*)(t-\tau^*)}}{2\pi} I^*(t).$$

Bearing in mind Lemma 2, since $b_1 < \alpha^*$ and since $\tilde{L}_0$, $\tilde{N}_0$ are zero for $t > 0$ big enough, it is evident that $\lim_{t \to +\infty} \Omega(t) = 0$.

Also, notice that estimation (16) provides, for $t > 0$ big enough and for some constant $K^* > 0$:

$$|\Omega(t)| \leq K^*[\|l_0\|_{L^1(w_0, w^*)} + \|n_0\|_{L^1(0,a^*)}].$$

The theorem is proved. □

3.1. Asymptotic behavior of solutions to the model (A)–(L)

Bearing in mind expression (4) together with the relationship $l(w^*, t) = l(w_0, t - \tau^*)E(\tau^*)$ valid for $t > \tau^*$, the densities of larvae and adults can be expressed in terms of $R(t)$ as:

$$\begin{aligned} l(w,t) &= \frac{E(\tau(w))}{E(\tau^*)} R(t + \tau^* - \tau(w)) \quad t > \tau^* \\ n(a,t) &= g(w^*) R(t-a) e^{-\int_0^a \mu(s)\, \mathrm{d}s} \quad t > a^* \end{aligned}$$

which provide immediately the following result:

COROLLARY 1. *The asymptotic behavior of the densities of larvae and adults is given by:*

$$\lim_{t\to+\infty} e^{-\alpha^* t} l(w,t) = C^*(l_0,n_0)\frac{E(\tau(w))}{E(\tau^*)}e^{-\alpha^*\tau(w)}$$
$$\lim_{t\to+\infty} e^{-\alpha^*(t-\tau^*)} n(a,t) = g(w^*)C^*(l_0,n_0)e^{-(\alpha^* a+\int_0^a \mu(s)\,\mathrm{d}s)}.$$

Theorem 2 allows us to establish a long-time estimation for the total population of larvae and adults, which are defined, respectively, by:

$$L(t) := \int_{w_0}^{w^*} l(w,t)\,\mathrm{d}w \quad \text{(larvae)}; \quad N(t) := \int_0^{a^*} n(a,t)\,\mathrm{d}a \quad \text{(adults)}.$$

That is, straightforward calculations provide, for $t > 0$ big enough, and some positive constants M_i, $i = 1, 2$:

$$|L(t)| \le M_1 e^{\alpha^* t}[\|l_0\|_{L^1(w_0,w^*)} + \|n_0\|_{L^1(0,a^*)}]$$
$$|N(t)| \le M_2 e^{\alpha^*(t-\tau^*)}[\|l_0\|_{L^1(w_0,w^*)} + \|n_0\|_{L^1(0,a^*)}].$$

These results show an exponential growth of the densities of larvae and adults as well as the total populations, determined by the constant α^*, solution to (10).

Let us say a few words about the constant $C^*(l_0, n_0)$, bearing in mind that we have restricted our calculations to nonnegative initial data l_0, n_0.

First, notice that $C^*(l_0, n_0) = 0$ if and only if $\hat{H}(\alpha^*) = 0$, which holds if and only if $L_0(t) = 0$ a.e. $t \in [0, \tau^*]$ together with $N_0(a) = 0$ for all $a \in [0, a^*]$. Our aim is to investigate whether there are nonnegative and nonzero initial data l_0, n_0 for which $C^*(l_0, n_0) = 0$. It is easy to see that $L_0(t) = 0$ a.e. $t \in [0, \tau^*]$ if and only if $l_0(w) = 0$ a.e. $w \in [w_0, w^*]$.

Regarding the function N_0, the result depends on the support of function β, $\mathrm{supp}\,(\beta) := [a_1, a_2]$, $0 \le a_1 < a_2 \le a^*$. We have:

LEMMA 3. *If $a_2 < a^*$, then $N_0(a) = 0$ for all $a \in [0, a^*]$ if and only if supp $(n_0) \subset [a_2, a^*]$.*
If $a_2 = a^*$, then $N_0(a) = 0$ for all $a \in [0, a^*]$ if and only if $n_0(a) = 0$ a.e. $a \in [0, a^*]$.

Proof. We only carry out the proof for the case $a_2 < a^*$, the result for $a_2 = a^*$ being an easy consequence.

It is evident that $N_0(a) = 0$ for all $a \in [a_2, a^*]$, so that let us assume that $a \in [0, a_2]$. Recall that:

$$N_0(a) = E(\tau^*)\int_a^{a_2} \frac{1}{g(w_0)}\beta(s)e^{-\int_{s-a}^{s}\mu(\sigma)\,\mathrm{d}\sigma} n_0(s-a)\,\mathrm{d}s$$

therefore, $N_0(a) = 0$ if $n_0(s) = 0$ for all $s \in [0, a_2 - a]$. Since a varies in $[0, a_2]$, this implies that $N_0(a) = 0$ for all $a \in [0, a_2]$ if and only if $n_0(a) = 0$ a.e. $a \in [0, a_2]$, as we wanted to prove. □

The conditions $L_0 = 0$ and $N_0 = 0$ in expression (5) imply that $R(t) = 0$ for all $t \ge 0$, and therefore, $l(w, t) = 0$ for all $t \ge \tau^*$ and also $n(a, t) = 0$ for all $t \ge a^*$. That is, the previous lemma provides a condition for extinction of both populations in a finite time, which has a not surprisingly biological meaning: Population (A)–(L) will be extinguished if and only if initially there is no population of larvae and if adults are too old to be fertile.

Let us say a few words about the statement *if* of the condition for extinction in a finite time of populations of larvae and adults. This means that there exists $t_0 > 0$ such that for all $t \ge t_0$ we have that $l(w, t) = 0$ a.e. $w \in [w_0, w^*]$ and also that $n(a, t) = 0$ a.e. $a \in [0, a^*]$, which in turn implies that $R(t) = 0$ for all $t \ge 0$ big enough. Therefore, if extinction in a finite time of both populations occurs, Theorem 2 leads to the condition $C^*(l_0, n_0) = 0$ and then Lemma 3 applies.

4. Conclusion

In this work, we study a linear system of hyperbolic partial differential equations, (A)–(L), with boundary and initial conditions. The system represents a model of a structured population based on the classical linear Lotka–MacKendrick model. The specificity of the proposed model lies in treating a population classified into two stages with different structuring variable for each one. The stages are called larval and adult though they could also be assimilated to the widespread terminology juvenile–adult. The larval stage is structured by weight so that the model can take into account that maturation occurs at a larval threshold. The adult stage is simply structured by age.

Generalizing what happens in simpler models for density-independent population growth [8,9,14], we prove in Corollary 1 that asymptotically the population will grow exponentially and that the larvae weight and adult age distributions will stabilize. To prove this result, the original system (A)–(L) is reduced to a delayed renewal equation with constant delay for the density of larvae at the maturation threshold, which asymptotic behavior is found via Laplace transform methods in Theorem 2.

The population either grows or declines exponentially depending on number α^* being positive or negative. Constant α^* is the only real solution (Proposition 1) of Eq. (10) which plays the role of characteristic equation of the functional equation (5). The net reproduction rate Γ_0 defined in (7) is larger or smaller than one if and only if α^* is positive or negative, respectively. This means that the expected number of offspring produced by one individual during her reproductive life, being larger or smaller than one, decides whether the population grows or declines exponentially. The expression of parameter Γ_0 is composed of two factors, one of them, $\int_0^{a^*} \beta(a) \exp(-\int_0^a \mu(s) \mathrm{d}s) \mathrm{d}a$, describing the expected number of offspring produced by an adult, and the second one, $\exp(-\int_{w_0}^{w^*} (\nu(w)/g(w)) \mathrm{d}w)$, measuring the probability that a new recruited larva survives till maturation weight. This last term is the key to analyze the influence on the population asymptotic behavior of particular forms of the growth rate together with different values of the maturation threshold. Note that this discussion could also be important for the analysis of equilibria in density-dependent models as well, since the environment at equilibrium could also be considered constant in time.

The complex model in [4] that originates the linear model (A)–(L) in this work describes the growth of a population of fish focussing on density-dependent effects at the larval stage, and in spite of its complexity, it takes into account no spatial effects. Starting from our simplified model, we plan to transform it into a spatially explicit one. In a previous work [3], which is a precedent of [4], a fish species which is subject to industrial fishing is studied: Solea solea, the common sole of the Bay of Biscay. The proposed model distinguishes different structured stages, as in [4], but pays no special attention to the larval stage. On the other hand, it includes the migration of the sole from its spawning grounds to the nursery grounds essentially as a horizontal diffusion process taking place during the larval stage. This migration is not the only movement the sole larvae undergo, they also move 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. In [3], these vertical migrations are averaged throughout the whole water column to produce a supposedly constant shoreward velocity. In [5], it is presented a simple age-structured model that includes the phenomenon of vertical migrations through a spatial structure of horizontal layers where demographic parameters change across it. A rigorous treatment of averaging in this framework is undertaken by considering vertical motion a fast process compared with the demographic process. This means that after averaging has been performed, using the so-called aggregation method, the model at hand is age-only dependent.

Research toward including in model (A)–(L) at the larval stage a horizontal diffusion process and vertical motion at possibly different time scales is planned following previous works [5,17].

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