Contents

Chapter 1

Introduction

1.1 History of the problem

Obviously, there exists a mutual relation between the human being and the Universe which is characterized by its diversity. On the other hand, we can see that each one is affected and influenced by the others. So, it is extremely interesting to study systematically, from the biological or ecological point of view, the Universe. Thus, we are urged to look for the natural laws and the evolution that govern all vegetable and animal creatures living in our universe. Despite the fact that mathematics are used as a language by any science in general and by the biology in particular, there is no doubt that the quantitative aspects of the latter are the most easily expressable by means of mathematical concepts.

In this respect, in 1798 [58], Malthus proposed a model of population dynamics. The solution of this problem is an exponential function. This is called the exponential growth of a malthusian population. Later on, in 1838 Verhulst [82] proposed a more realistic model of population growth for the study of the dynamics of a unique population. This model is known as the logistic equation and it improves the Malthus model by including competition for resources. A system of two equations, for the study of the prey-predator interaction, was proposed independently by Lotka in 1925 [54] and Volterra in 1926 [83].

The dynamics of the different vegetable or animal populations is affected by the structure ot those populations with respect to some internal variables (age, size, social rank, etc). Many authors have extensively developed the theory of continuous structured populations dynamics. The density and the birth and death rates, for example, of one population may change according to the different life cycle stages it passes. This means that the characteristics of organisms usually vary as they age. The age-structured population models have been one of the most important theories in this development. Continuous time formulations of age-structured population models lead to partial differential equations for the population density, $u(a,t)$, the density of individuals of age a at time t. The study of these continuous models incorporating age effects was initiated by Sharpe and Lotka (see [75]) in 1911 and pursued by McKendrick [60] in 1926. In these models, birth and mortality rates are linear functions of the population densities because they depend only on the age. This implies the linearity of the equations, i.e. they are malthusian in some sense, but the age-structure implies that the individuals are not considered identical. In 1959 [84] Von Foerster was the first author to express these by means of partial differential equations

$$\begin{cases} u_t + u_a &= -m(a)u, \\ u(0,t) &= \int\limits_0^\infty \beta(a)u(a,t)da, \\ u(a,0) &= u_0(a), \end{cases} \tag{1.1}$$

where $a \in [0,\infty), t > 0, m(a)$ is a nonnegative function of age known as the age specific mortality modulus and $\beta(a)$ is a nonnegative function of age called the age specific fertility modulus (see [86]).

From the physical point of view the first equation of (1.1) gives the balance-law of the members of the population (or aging process of the population). In the case $m(a) = 0$, it reduces to an equation of conservation (in this case mass conservation). The second equation gives an idea about the birth process of the population, i.e., it satisfies the so-called birth law (see [86]). Moreover, the expression $u(0,t)$ may be interpreted as the birth rate at time t. The third equation gives the initial age distribution of the population. Finally, $u_0(a)$ is a nonnegative function of age a, which yields the initial state of the population.

In 1974, a first nonlinear version of Problem (1.1) was introduced by Gurtin and MacCamy in [33], incorporating the density dependence in the fertility coefficient and the mortality coefficients of the population. Thus, $\beta(a,P)$ and $m(a,P)$ are now nonnegative functions of two independent variables a and P, where P stands for the total population at a given time $P = P(t) = \int_0^\infty u(a,t)dt$ which is the total population. This means that there exists a competition for resources between the individuals of the population via the birth and death rates. The model as reads

$$\begin{cases} u_t + u_a + m(a,P(t))u &= 0, \\ u(0,t) &= \int_0^l \beta(a,P(t))u(a,t)da, \\ u(a,0) &= u_0(a), \end{cases} \tag{1.2}$$

where $a \in [0,\infty]$ and $t > 0$. The boundary condition is also nonlinear which causes difficulties in solving this problem (see [76]). This model and similar nonlinear models have been investigated by many researchers who used the method of lines to reduce the model to a system of Volterra integral equations. Via a fixed point argument applied to the problem along the characteristics Chipot (see [19]) proved in 1983 existence and uniqueness of solution to a problem like (1.2) in which $P(t)$ had been substituted more general formulation of the population state,

$$Q(t) = \int_0^\infty k(a,t)u(a,t)\,da$$

where k is such that $|k(a,t)| \le |C(T)|$ *a.e.* and $(a,t) \in \mathbb{R}^+ \times [0,T]$.

Along these lines many authors have proposed age-dependent population models of two interacting biological species (two species in competition or two species as predator and prey). For instance, in 1931 Bailey proposed the first prey-predator model, namely a model of a interaction between hosts and parasites, with an age structure (see [11]).

In 1975 Hoppensteadt [45] formulated a genetic age-dependent population model. He considered the case of one locus on a chromosome at which the gene has two or more different alleles. A similar model was studied by Webb in [86]. Thus, conditions under which such a population is driven to extinction were determined.

The age structure is an important consideration in the design of the models which describe the evolution of infectious diseases since several factors as exposure, susceptibility immunity, inoculation and quarantine are frequently affected by this continuous variable (see [86]). Thus, Hoppensteadt in [44] and Dietz in [27] are among the first authors who proposed continuous deterministic epidemic models incorporating age effects. In [28] Dietz and Schenzle proposed an age-dependent model with proportionate mixing, constant population size and complete immunization. In this context, Hadeler and Müller studied in 1995 a vaccination model in an age-structured population (see [36, 37]). They considered a situation where the population is in demographic equilibrium and the vaccination strategy is stationary.

Age and size dependent population systems have been also used to model cell proliferation and tumor growth (see the works of Arino and Kimmel [6, 7] and more recently by Arino et al. [10])

Age effects have also been considered in several optimal harvesting models (see [3, 12, 34, 35, 63, 69, 71, 72]).

The dynamics of the populations depend frequently on the environment where they move. Thus, many researchers generalized the model (1.1) introducing a spatial diffusion term. They take $u(a, x, t)$ as the distribution of individuals having age $a > 0$ at time $t > 0$ and position x in a bounded domain (see ([13, 32, 50, 55]). Mathematically, the solution of (1.1) is in the phase space $C([0, T], L^1(0, l))$. However, considering the spatial diffusion the natural phase space would be $C([0, T], L^1((0, l), L^2(\Omega)))$.

1.2 Motivation of the problem

Some mathematical models in ecology have the form

$$\begin{cases} x' &= A(l, r)x \\ r' &= F(l, r, x) \end{cases} \tag{1.3}$$

where $'$ stands for the derivative with respect to time and x stands for the population density or population vector of a predator (or consumer) species feeding on a resource or a collection of resources whose amount is given by the vector r. Often x takes values in an infinite dimensional space X; this is so when x represents the density of a population structured by a continuous variable as age or size whereas one assumes that r is an $n-$dimensional vector, each component being the total quantity of a given resource.

$A(l,r)$ is a linear operator which is assumed to generate a positive semigroup and to have a "dominant "simple real eigenvalue $\lambda(l,r)$ in the sense that any other spectral value of $A(l,r)$ has a real part less than some number $\omega < \lambda(l,r)$. The number $\lambda(l,r)$ is sometimes called the population growth rate or the malthusian parameter. Typically, $\lambda(l,r)$ is an increasing function of each component of r. Moreover we assume that the corresponding eigenvector $\varphi(\lambda,r)$ is the only nonnegative eigenvector of $A(l,r)$. The real parameter l characterizes the individuals of the population and summarizes the relevant features under study from an evolutionary point of view. In general it is what is sometimes called an evolutionary continuous variable, say for instance a physical measure (body) size or a physiological feature or a life-history strategy (like maturation age), genetically fixed and submitted to evolution by mutation and selection (see [64]).

On the other hand, the value of r, which for a given l determines the population growth rate, is often called the environment observed (felt) by the predator population.

We are mainly interested in nonzero predator population steady states. Biological meaning (nonnegativity of densities) obviously imposes that these steady states are scalar multiples of the nonnegative eigenvector corresponding to 0 eigenvalue of $A(l,r)$. So the equilibrium equations reduce to the $(n+1)-$dimensional system

$$\left\{ \begin{array}{lcl} \lambda(l,r) & = & 0, \\ F\left(l,r,c\varphi(l,r)\right) & = & 0, \end{array} \right. \tag{1.4}$$

for the $n+1$ unknowns $c(l), r_1(l), ..., r_n(l)$.

In this context, a value $\hat{l}$ of the evolutionary variable l is called a (local) E.S.S. (evolutionary stable strategy or evolutionary unbeatable strategy, see [64]) if there is a solution of (1.4) with $l = \hat{l}$ (a steady state of (1.3) when $l = \hat{l}$) such that $\lambda(l, r(\hat{l})) < 0$ for all $l \neq \hat{l}$ (for all $l \neq \hat{l}$ in a neighborhood of l). So, $\hat{l}$ is an E.S.S. if the population growth rate of a "mutant " of type l is negative (it becomes extinct) when the environmental conditions are the ones of the steady state of the "resident" population of type $\hat{l}$. This is quoted by saying that the $\hat{l}$ strategy can not be invaded but this assumes a dynamics for the enlarged system obtained for the populations of types $\hat{l}$ and l and for the resources and an initial condition with small population of type l.

It is worth noting that it seems reasonable to require additionally asymptotic stability of $\left(c(\hat{l})\varphi(\hat{l}, r(\hat{l}))\ ,\ r(\hat{l})\right)$ as a steady state of the "ecological" system (1.3) with $l = \hat{l}$. On the other hand, some authors have extended the definition of E.S.S. to the case of systems with more complicated attractors such as periodic orbits or even strange attractors (see [68, 29]).

A special case of system (1.3) which we will consider in the forthcoming is obtained assuming that environmental conditions modify the growth rate of the predator population in a uniform way. A mathematical formulation of this assumption consists in assuming the following special form of the operator $A(l, r)$:

$$A(l, r) = A(l) - m(r)I, \tag{1.5}$$

where $m(r)$ is a scalar function and I is the identity operator. Then we have for the population growth rate, $\lambda(l, r) = \lambda(l) - m(r)$ where $\lambda(l)$ is the dominant eigenvalue of $A(l)$ and (1.4) reduces to

$$\left\{ \begin{array}{rcl} \lambda(l) - m(r) & = & 0, \\ F\left(l, r, c\varphi(l)\right) & = & 0. \end{array} \right. \tag{1.6}$$

Now the E.S.S. condition for l can be written as

$$\lambda(l) - m(r(\hat{l})) < 0 (= \lambda(\hat{l}) - m(r(\hat{l})))$$

if $l \neq \hat{l}$ (in a neighborhood of $\hat{l}$ in the local case). Equivalently, $\lambda(l) < \lambda(\hat{l})$ if $l \neq \hat{l}$. So, $\hat{l}$ is an E.S.S. if there is a (asymptotically stable with respect to system (1.3) when $l = \hat{l}$) solution of ((1.6); $l = \hat{l}$) and moreover, $\hat{l}$ is a (local) strict maximum point of the real function $\lambda(l)$. This is Corollary 2 in [26] or Result 2 in [64].

On the other hand,the assumption (1.5) has another important advantage related with the dynamics of Problem (1.3) , namely, it provides the solution of the initial value problem for (1.3) ($x(0) = x_0$, $r(0) = r_0$) in the form $\left(\psi(t)\tilde{S}(t)x_0, r(t)\right)$ where $\tilde{S}(t)$ is the linear semigroup generated by the operator $\tilde{A}(l) = A(l) - \lambda(l)I$ whereas $(\psi(t), r(t))$ is the solution of the following system of ordinary differential equations (cf [61], Part A, chap. IV. 5.2)

$$\begin{cases} \psi' &= (\lambda(l) - m(r))\,\psi \quad , \quad \psi(0) = 1, \\ r' &= F\left(l, r, \psi\tilde{S}(t)x_0\right) \quad , \quad r(0) = r_0. \end{cases} \tag{1.7}$$

Moreover, the hypotheses on $\tilde{A}(l)$ imply that (1.7) is an asymptotically autonomous system and so, the asymptotic behaviour of the solutions of (1.3) can be easily studied at least when r is one dimensional.

Mylius and Diekmann consider in [64] an example where $x(t)$ is a population distributed into two groups: the juveniles, with a population structured by age, and the adults. The evolutionary variable in this example is the maturation age which we call l and we assume to take values in $[0, \infty)$. The juveniles have a death rate $m(r)$, which can be assumed to decrease with r, and adults have a fertility modulus $b(l)$, assumed to increase with the maturation age and a death rate $\nu + m(r)$ where ν is a constant larger than $-m(\infty)$ ($m(\infty) > 0$ is the limit of $m(r)$ when the amount of resources tends to infinity, i.e., in the virgin environment, see [64]). The model equations read as follows:

$$\begin{cases} u_t + u_a &= -m(r)u(a,t), \\ v' &= u(l,t) - (\nu + m(r))v, \\ r' &= (g(r) - h[L(u,v)])r, \\ u(0,t) &= b(l)v(t), \\ u(a,0) &= u_0(a), \quad v(0) = v_0, \quad r(0) = r_0, \end{cases}$$

for a density of juveniles $u(a,t), a \in [0,l]$ and an adult population number $v(t)$. Moreover, we will assume in the following sections that $g(r)$ decreases and vanishes for some r_c (which gives a logistic like behaviour of the resources population in the absence of predators) and an increasing and unbounded function h, vanishing at 0, and L being a positive continuous linear functional (which gives a simple predation term). In this situation $\lambda(l)$ is the unique real solution of the equation

$$b(l) - (\lambda + \nu)e^{\lambda l} = 0. \tag{1.8}$$

Let us further assume some hypotheses on the function $b(l)$, namely $b(0) = 0, b(l) \geq 0$ and that $(\ln b(l))'$ is a strictly decreasing function with limit 0 when l tends to infinity (notice that this last hypothesis despite its technical appearance, is not so much restrictive and it implies $b'(l) > 0$ and it allows polynomial but not exponential growth). Under the previous hypotheses, we can state

Proposition 1.1. *There is an E.S.S. $\hat{l}$ if and only if $b(l) > \nu$ for some l and $\lambda(\hat{l})$ belongs to the interval $(m(r_c), m(0))$. Furthermore, the E.S.S. is unique whenever it exists and it is a solution of equation (1.8) with λ substituted by $b'(l)/b(l)$.*

Proof. About equation (1.8), first notice that $\lambda(0) = -\nu$ and that $\lambda(l) > -\nu$ for $l > 0$. (1.8) clearly implies that $\lambda(l)$ is positive if and only if $b(l) > \nu$. So there is no solution of system (1.6) (i.e., there is no non-trivial steady state) when $b(l)$ is bounded above by (a necessarily positive) ν. So in this case there is no place to talk about equilibrium E.S.S.

Now taking the implicit derivative with respect to l in (1.8) we obtain, for $l > 0$,

$$b(l)\left(\frac{b'(l)}{b(l)} - \lambda(l)\right) - \lambda'(l)\left(lb(l) + e^{l\lambda(l)}\right) = 0. \tag{1.9}$$

If $b(l)$ takes values larger than ν (so $\lambda(l)$ becomes positive), then the function $f(l) := b'(l)/b(l) - \lambda(l)$, which is positive for small l, necessarily changes signs (because $b'(l)/b(l) = (\ln b(l))' \longrightarrow 0$ as $l \longrightarrow \infty$ and f and λ' have the same sign) and it can not vanish again because $f(l) = 0$ implies $\lambda'(l) = 0$ and so $f'(l) < 0$ due to the hypothesis about $b'(l)/b(l)$ being decreasing. So $\lambda(l)$ has a unique critical point $\hat{l}$ which is a strict absolute maximum (here the log $-$concavity of the function $b(l)$ plays an essential role and the elimination of this hypothesis allows the existence of several local E.S.S.'s). Finally, $\hat{l}$ is the (unique) E.S.S. if $m(0) > \hat{\lambda} := \lambda(\hat{l}) = b'(\hat{l})/b(\hat{l}) > m(r_c)$ and if $\hat{\lambda} < m(\infty)$ there is no non-trivial steady state for any l (and, a fortiori, there is no E.S.S.). If $\lambda(\hat{l}) > m(0)$ the existence of non-trivial steady states is possible for some values of $l \neq \hat{l}$ (see, Sec. 3.3) but there is no E.S.S. and the system has little biological sense. $\square$

Up to now we have assumed a fixed " intrinsic adult death rate" ν. Nevertheless, the above analysis allows us to consider the function $\hat{l} = \hat{l}(\nu)$ for $\nu \in (-m(\infty), b(\infty))$, where $b(\infty)$, possibly equal to $+\infty$, means the limit of $b(l)$ as l tends to ∞. Let us compute $\hat{l}'$. Taking the implicit derivative in (1.8) and (1.9) with respect to ν (now thinking of λ as a function $\lambda(\nu, l)$), and using $\frac{\partial\lambda(\nu,\hat{l})}{\partial l} = 0$ gives

$$\frac{\partial^2\lambda(\nu,\hat{l})}{\partial\nu\partial l} = \left(1 + \hat{l}(\hat{\lambda} + \nu)\right)^{-2}(\hat{\lambda} + \nu)$$

which is always positive. So, as $\partial^2\lambda(\nu,\hat{l})/\partial l^2 \leq 0$ because $\hat{l}(\nu)$ is a maximum point of the function $l \longrightarrow \lambda(\nu, l)$, we conclude that $\hat{l}(\nu)$ is an increasing function, i.e. *an increase in the "intrinsic" mortality of adults causes a larger value of the evolutionary stable maturation age* $\hat{l}$. This fact could for instance be related to an evolutionary explanation of the extremely short adult life of some insect species with a comparatively long life as larvae.

On the other hand, as $\lambda(\nu, l) < 0$ if $b(l) < \nu, \nu$ tending to $b(\infty)$ obviously implies $\hat{l}(\nu) \longrightarrow \infty$ and $\hat{\lambda}(\nu) = \lambda(\hat{l}(\nu)) = b'(\hat{l}(\nu))/b(\hat{l}(\nu)) \longrightarrow 0$. That is *a larger intrinsic adult mortality is only compatible with a small* $m(r_c)$ (because $\hat{\lambda}$ has to be larger than $m(r_c)$)*and causes a very large optimal maturation age.*

As particular although illustrative examples, we can consider two specific fertility functions: $b(l) = cl$ for some constant c (unbounded birth as l tends to infinite) and $b(l) = l/(1 + l)$ (bounded birth rate). In the first case one explicitly obtains

$$l_{ESS} = \frac{e\nu}{2c} + \sqrt{\left(\frac{e\nu}{2c}\right)^2 + \frac{e}{c}}.$$

(notice $\hat{\lambda} = b'(\hat{l})/b(\hat{l}) = 1/c\hat{l}$ and use (1.8)) whereas in the second one (assuming, for simplicity $\nu = 0$) $\hat{l}$ satisfies the equation $l^2 = e^{\frac{1}{1+l}}$ which has an approximate solution 1.25 ($\hat{\lambda} = b'(\hat{l})/b(\hat{l}) = 1/\hat{l}(1 + \hat{l})$ and use (1.8)). Taking $\nu = 0$ and $c = 1$ in the first case, allows a comparison with the second one that gives larger value of the E.S.S. ($\sqrt{e} > 1.25$) as could be expected from the unboundedness of $b(l)$ in the first case.

1.3 Main results

In this thesis, a continuous age-structured population model with two population groups, juveniles and adults, and with a dynamics for a one dimensional resource, is considered.

In Chap. 2, the initial value problem (2.1) is studied without the assumption of the uniform increase of mortality case. This is of course biologically relevant when modelling biological species with, for instance, metamorphosis.

Nevertheless, since the nonlinearities do not affect the birth rate, the model fits in the standard theory of semilinear equations in Banach spaces (see [65], for instance) from the point of view of existence and uniqueness of solutions. This avoids the need to use the much more general setting involving the theory of dual semigroups as developed in [25].

Firstly, we show that the operator B, which represents the linear part of Problem (2.1), is the infinitesimal generator of a positive C^0 semigroup $\{T(t), t \geq 0\}$. This asserts that the initial value problem (2.1) generates a dynamical system. We also prove that the operator B has a dominant real eigenvalue. After that, we deal with the semilinear formulation of the initial value problem and we give a result on local existence and uniqueness. We also show continuous dependence of mild solutions of Problem (2.1) on initial age distributions. Later, using the positivity of the solutions, global existence is proved. Let us also remark that Theorem 2.3 establishes smoothness with respect to time of the total population in the linear problem, even for only integrable initial conditions. Finally, a rather explicit description of the set of equilibria, depending on the (constant) birth rate is given. And we prove that there is a unique nontrivial equilibrium (u_e, v_e, r_e), whenever $b \in \left(m_2(r_c)e^{\int_0^l m_1(a,r_c)\,da}\,,\, m_2(0)e^{\int_0^l m_1(a,0)\,da}\right)$. Moreover $0 < r_e < r_c$.

In Chap. 3, the only density dependence is through a uniform increase of the death rates. We describe the complete "ecological" dynamics of this model for given values of the maturation age l. Section 3.2 is devoted to reducing Problem (2.1) to a nonautonomous ordinary differential system. Here, in Theorem 3.5, an important role is played by the fact that the semigroup has asynchronous exponential growth, i.e., there exists a strictly dominant eigenvalue and a rank one spectral projection (see [86] and, for a cell population dynamics application, [8]). So, the problem is related to System (3.5) and the solution is obtained in the form mentioned in Section 1.2. In Section 3.3 we analyze the asymptotic behaviour of the solutions. The special form of the solutions reduces the problem to the study of an asymptotically autonomous system of two ordinary differential equations (see System 3.5). This is done using results by Markus (see [59], [81], [62]), which, under some hypotheses, relate the asymptotic behaviour of the solutions to that of the limit system. An important goal in this respect is to prove that the solutions are bounded forward (see Prop. 3.4). The limit system behaviour is established by means of a standard application of the Poincaré-Bendixson theorem and a Lyapunov function. More recently [81] and [62] generalize Markus results to the case of asymptotically autonomous semiflows in infinite dimensional spaces.

The main result of Section 3.3 is Theorem 3.11 where the existence of a global attractor reduced to a coexistence equilibrium point is proved if $\tilde{g}(r) = r$ and the adult fertility b belongs to the interval $\big(m_2(r_c)e^{m_1(r_c)l}, m_2(0)e^{m_1(0)l}\big)$; here, m_1 and m_2 stand for the juvenile and adult death rates, respectively. Notice that the left endpoint of this interval is small if the death rates are small when the amount of resources equals the environmental capacity r_c, and that the right endpoint is large if the death rates are large when there is no resource. The first condition is needed in order to avoid extinction of the consumer species whereas the second one has an obvious biological meaning.

In Chap. 4, model (2.1) is undertaken without the assumption of uniform increase of mortality. In this chapter, the reduction of (2.1) to a nonautonomous ordinary differential system is no longer possible and more general methods are needed. We take advantage of the semilinear formulation through the variation of constants formula to obtain some asymptotic results and, mainly, to show smoothing properties of the system, already known for similar equations (see [86] for the age dependent case, and [18] for the size dependent one) but always obtained with more difficult proofs.

The chapter is organized as follows. In Section 4.1 a study of the neighbourhood of the non-coexistence equilibria is also done, and a local result on stability of the coexistence equilibrium is performed via bifurcation theory. Let us remark also that Theorem 4.1 proves smoothness of the total population which is used later in Section 4.3.

Section 4.2 deals local stability and instability of the existence equilibrium. It contains analytical results on the stability region of this equilibrium in the parameter space, including Theorem 4.7, which in particular states that the coexistence equilibrium is stable whenever the death rates of young and adult populations have equal derivatives at the coexistence equilibrium. This agrees with the results of Theorem 3.11 and it is a generalization of these results with respect to the local stability analysis. On the other hand, loss of stability arises by the crossing of the imaginary axis by a conjugate pair of eigenvalues. This can generate a Hopf bifurcation of periodic solutions close to the equilibrium. Some numerical computations on the stability curves (i.e., on the boundary of the stability region) for particular values of the parameters are also presented in Subsection 4.2.3.

Finally, since a complete analytical description of the dynamics does not seem possible in this case, we use the smoothing action of the nonlinear semigroup and its dissipativeness properties under suitable and not much more restrictive extra hypotheses, to prove the existence of a compact global attractor in the sense of ([39]). The description of this attractor is also given in some cases. The idea behind the proof of dissipativeness is borrowed from [15] (see also Section 3.3), namely, the construction of a collection of bounded positively invariant regions based on the total population numbers of consumers and resources. As we have already said, the model in [15] (see also Chap. 3) is asymptotically reduced to a two dimensional dynamical system whereas here only a system of two differential inequalities is obtained (see (4.18)). This explains why the conclusions on global dynamics are now weaker than in ([15]).

Recall that removing, in Chap. 4, the hypothesis of the uniform increase of mortality destroys the algebraic structure

$$x' = Ax - m(r)x,$$

and it is not possible to give a complete analytical description of the dynamics of Problem (2.1). The goal of Chap. 5 is the study of the stability of the coexistence equilibrium point of Problem (2.1) perturbing the death rate of the juveniles, $m_1(r) = m_2(r) + constant$, by a function $\varepsilon(a, r)$ which depends on the age and the amount of the resources. We first prove that the dominant real eigenvalue λ^* of the operator A is simple and the coexistence equilibrium point (u_e, v_e, r_e) of the initial value problem (2.1) is hyperbolic. Later, we give a condition which guarantees existence of the coexistence equilibrium point of the perturbed problem (5.5). Theorem 5.3 is the main result of this chapter. It gives an explicit condition, depending only on the parameter functions of the problem, about the norm of the function $\varepsilon(a, r)$, so achieving the objective of this chapter. In order to prove this result we write the linearization of (5.5) at its coexistence equilibrium point $(u_\varepsilon, v_\varepsilon, r_\varepsilon)$ as the sum of the linearization of (2.1) at (u_e, v_e, r_e) and another term. This allows us to apply [48, Theorem 3.17].

In the last chapter we use a numerical implicit method to study the stability of the coexistence equilibrium point of Problem (2.1). Subsect. 6.2.1 illustrates the adaptation of an implicit method, which is presented in [79], to our problem in order to study numerically the asymptotic behaviour of the solutions of (2.1). In Subsect. 6.2.2, we study two examples and we present numerical results. This work requires to assume in the forthcoming somehow special forms for some functions of our problem. Both examples illustrate that the linear implicit scheme and the Fortran program work a satisfactory way. The numerical results obtained are coherent with all results given in the other chapters studying the stability of the coexistence equilibrium point of Problem (2.1). We give some remarks about these results and about the Fortran program which we use.

Finally, we give conclusions and discuss some remarks.

Chapter 2

Initial Value Problem for a Semilinear Equation

2.1 Introduction

The purpose of this chapter is to investigate the initial value problem (2.1) without the assumption of the uniform increase of mortality. We first set the age-dependent model which is a nonlinear partial differential equation coupled to two ordinary differential equations. We analyze the linear part of the model and we show that it generates a positive C^0-semigroup. The semilinear formulation in the treatment of an age-structured population dynamics model is exploited from the view point of existence and uniqueness of a positive solution. Finally, an explicit description of the set of equilibria is given in terms of the birth rate b taken as a parameter.

2.2 Setting for the age-dependent model

We consider a mathematical model of a population subdivided into two groups: the juveniles, with density $u(a,t)$, where $a \in [0,l]$ denotes the age and l denotes maturation age, and the adults with a population number $v(t)$. The juveniles have a death rate $m_1(a,r)$ which is assumed to be continuous with respect to a and to strictly decrease with respect to the amount of available resources $r(t)$ at time t. The adults have a fertility rate b and a strictly decreasing death rate $m_2(r)$. The model system reads as follows:

$$\begin{cases} u_t + u_a &= -m_1(a,r)u, \\ v' &= u(l,t) - m_2(r)v, \\ r' &= g(r)r - h(L(u,v))\tilde{g}(r), \\ u(0,t) &= bv(t), \\ u(a,0) &= u_0(a), \quad v(0) = v_0, \quad r(0) = r_0. \end{cases} \tag{2.1}$$

Furthermore, we assume that both death rates are smooth and have positive lower bounds and that they are bounded above. We also assume that $g(r)$ is a smooth decreasing function which vanishes at some $r_c > 0$, that $\tilde{g}(r)$ is a increasing and smooth function which vanishes at 0, h is a smooth increasing and unbounded function vanishing at 0 and L is a positive continuous linear functional i.e $L(u,v) > 0$ if $u \geq 0$, $v \geq 0$ and moreover $(u,v) \neq (0,0)$. Also, $h(L(u,v))$ is the amount of the resources consumed by the predator population per unit of time and resources.

The theory of semilinear equations will be used to resolve Problem (2.1). So we write it in the following abstract form:

$$\begin{cases} \begin{pmatrix} u \\ v \\ r \end{pmatrix}' &= B\begin{pmatrix} u \\ v \\ r \end{pmatrix} + f(u,v,r), \\ u(a,0) &= u_0(a), \quad v(0) = v_0, \quad r(0) = r_0, \end{cases} \tag{2.2}$$

where

$$B := \begin{pmatrix} -\frac{d}{da} & 0 & 0 \\ E_l & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

is an operator on the Banach space $Y := L^1[0,l] \times \mathbb{R} \times \mathbb{R}$ endowed with the norm $|\ |_Y := |\ |_{L^1[0,l]} + |\ | + |\ |$. The domain of B is $D(B) = \{(u,v,r) \in W^{1,1}[0,l] \times \mathbb{R} \times \mathbb{R}; u(0) = bv\}$. $E_l u := u(l)$ is the evaluation of u at age l and f is a nonlinear function on Y given by $f(u,v,r) := (-m_1(a,r)u\ ,\ -m_2(r)v\ ,\ g(r)r - h(L(u,v))\tilde{g}(r))$.

2.3 The linear problem

In this subsection and in the forthcoming one, let $\nu \in \mathbb{R}$ and let

$$A := \begin{pmatrix} -\frac{d}{da} & 0 \\ & \\ E_l & -\nu \end{pmatrix}$$

be an operator on the Banach space $X := L^1[0,l] \times \mathbb{R}$ with the norm $| \ |_X := | \ |_{L^1[0,l]} + | \ |$ and with domain $D(A) = \{(u,v) \in W^{1,1}[0,l] \times \mathbb{R} : u(0) = bv\}$.

Next we show that for any $\nu \in \mathbb{R}$, A is the infinitesimal generator of a positive C^0-semigroup $\{S(t), t \geq 0\}$, and therefore the operator B, defined at the end of Sec. 2.2, generates, as $\nu = 0$, the positive C^0-semigroup $\begin{pmatrix} S(t) & 0 \\ 0 & I \end{pmatrix} := T(t)$ where I is the real identity function. That is, the initial value problem generates a dynamical system. This result is showed here for any $\nu \in \mathbb{R}$ because we will need it in Sec. 3.2.

Below, we give a characterization of the spectrum of the operator A and we will show that it has a dominant simple real eigenvalue.

Finally, we will get a result concerning the growth rate of the predator population for the linear problem associated to (2.1).

We will use then the bound $\|T(t)\| \leq Me^{\omega t}$ for some $M \geq 1, \omega \in \mathbb{R}$ and for any $t \geq 0$.

The proof of the first result is based on the following lemmas:

Lemma 2.1. *Let $\{S_0(t), 0 \leq t \leq l\}$ be a family of bounded linear operators from X into X satisfying the properties of a C^0-semigroup on $[0,l]$. Then the operators $\{S(t), t \geq 0\}$ defined by*

$$S(t) = \begin{cases} S_0(t) & ; \quad 0 \leq t \leq l \\ S_0(l)^n S_0(r) & ; \quad t = nl + r \end{cases}$$

where $n \geq 1$ is a natural number and $0 \leq r < l$ is a real number, form a C^0-semigroup.

Proof. Initially it is obvious that

$$S(0) = S_0(0) = I,$$

$$\lim_{\substack{t \to 0 \\ t > 0}} S(t)u = \lim_{\substack{t \to 0 \\ t > 0}} S_0(t)u = u$$

and, for $t_1 + t_2 \leq l, S(t_1 + t_2) = S(t_1)S(t_2)$. Consequently it remains to prove this last equality for any $t_1, t_2 \geq 0$ such that $t_1 + t_2 \geq l$.

i) $t_1, t_2 \leq l$ and $t_1 + t_2 \geq l$.
If $t_1 = t_2 = l$ then $S(t_1 + t_2) = S(2l) = S_0(l)^2 = S(t_1)S(t_2)$. Else, we have $t_1 + t_2 = l + r,\ r < l$ and

$$\begin{aligned} S(t_1 + t_2) &= S_0(l)S_0(r) \\ &= S_0(l)S_0(t_1 + t_2 - l) \\ &= S_0(t_1)S_0(l - t_1)S_0(t_2 - (l - t_1)) \\ &= S_0(t_1)S_0(t_2). \end{aligned}$$

ii) $t_1 < l$ and $t_2 > l$.
Then there exist $n \in \mathbb{N}$ and $r \in \mathbb{R}$ such that $t_2 = nl + r$ and $r < l$. Therefore it follows that $t_1 + t_2 = nl + t_1 + r$ and

$$\begin{aligned} S(t_1 + t_2) &= \begin{cases} S_0(l)^n S_0(t_1 + r) & ; \ t_1 + r < l \\ S_0(l)^{n+1} S_0(t_1 + r - l) & ; \ t_1 + r \geq l \end{cases} \\ &= \begin{cases} S_0(l)^n S_0(t_1) S_0(r) & ; \ t_1 + r < l \\ S_0(l)^n S_0(l) S_0(t_1 + r - l) & ; \ t_1 + r \geq l \end{cases} \\ &= S_0(l)^n S_0(t_1) S_0(r) \\ &= S_0(t_1) S_0(l)^n S_0(r) \\ &= S(t_1)S(t_2). \end{aligned}$$

iii) $t_1, t_2 > l$.
It is obvious that there exist $n_1, n_2 \in \mathbb{N}$ and $r_1, r_2 \in \mathbb{R}$ such that

$$\begin{aligned} t_1 &= n_1 l + r_1 \qquad \text{with} \quad r_1 < l, \\ t_2 &= n_2 l + r_2 \qquad \text{with} \quad r_2 < l, \end{aligned}$$

that is $t_1 + t_2 = (n_1 + n_2)l + r_1 + r_2$ and therefore

$$S(t_1 + t_2) = \begin{cases} S_0(l)^{n_1+n_2} S_0(r_1 + r_2) & ; \ r_1 + r_2 < l \\ \\ S_0(l)^{n_1+n_2+1} S_0(r_1 + r_2 - l) & ; \ r_1 + r_2 \geq l. \end{cases}$$

Finally, using the first case, it follows that

$$\begin{aligned} S(t_1+t_2) &= \begin{cases} S_0(l)^{n_1}S_0(r_1)S_0(l)^{n_2}S_0(r_2) & ; \quad r_1+r_2<l \\ \\ S_0(l)^{n_1+n_2}S_0(l)S_0(r_1+r_2-l) & ; \quad r_1+r_2\geq l \end{cases} \\ &= S_0(l)^{n_1}S_0(r_1)S_0(l)^{n_2}S_0(r_2) \\ &= S(t_1)S(t_2)\square \end{aligned}$$

Lemma 2.2. *Let $p\in\mathbb{N}$ such that $1\leq p<\infty$. Then for any $u\in L^p([a,b])$ it follows that*

$$\lim_{|h|\to 0}\int_a^b |u(x+h)-u(x)|^p dx = 0.$$

Proof. If $u\in C_0^\infty([a,b])$ the proof is straightforward, else u can be approached by a sequence of functions of $C_0^\infty([a,b])$. $\square$

Theorem 2.1. *The linear operator A is the infinitesimal generator of a C^0-semigroup.*

Proof. A formal solution of the linear part of System (2.1) by the method of characteristics gives rise to the family of bounded linear operators on X, $\{S_0(t), 0\leq t\leq l\}$, such that

$$\begin{aligned} &S_0(t)(u_0,v_0)(a) \\ := &\begin{pmatrix} S_1(t)(u_0,v_0) \\ \\ S_2(t)(u_0,v_0) \end{pmatrix}(a) \\ = &\begin{pmatrix} \begin{cases} u_0(a-t) & ; \quad a>t \\ \\ bv_0e^{-\nu(t-a)}+b\displaystyle\int_0^{t-a} e^{-\nu(t-a-s)}u_0(l-s)ds & ; \quad a\leq t \end{cases} \\ \\ v_0e^{-\nu t}+\displaystyle\int_0^t e^{-\nu(t-s)}u_0(l-s)ds \end{pmatrix}. \end{aligned} \tag{2.3}$$

Firstly let us show that this family has the properties of a C^0-semigroup on $[0,l]$. Namely, for any $t_1, t_2 \geq 0$ such that $t_1 + t_2 \leq l$,

$$S_0(t_1)S_0(t_2)(u_0, v_0) = \begin{pmatrix} S_1(t_1)S_0(t_2)(u_0, v_0) \\ \\ S_2(t_1)S_0(t_2)(u_0, v_0) \end{pmatrix}$$

holds, let us prove then that

$$S_0(t_1 + t_2)(u_0, v_0) = S_0(t_1)S_0(t_2)(u_0, v_0). \tag{2.4}$$

It follows that

$$\begin{aligned}
& S_1(t_1)S_0(t_2)(u_0, v_0)(a) \quad = \\
= & \begin{cases} S_1(t_2)(u_0, v_0)(a - t_1) & ; \quad a > t_1 \\ bS_2(t_2)(u_0, v_0)e^{-\nu(t_1 - a)} + b\displaystyle\int_0^{t_1 - a} e^{-\nu(t_1 - a - s)} S_1(t_2)(u_0, v_0)(l - s)ds & ; \quad a \leq t_1 \end{cases} \\
= & \begin{cases} \begin{cases} u_0(a - t_1 - t_2) & ; \quad a > t_1 + t_2 \\ bv_0 e^{-\nu(t_1 + t_2 - a)} + b\displaystyle\int_0^{t_1 + t_2 - a} e^{-\nu(t_1 + t_2 - a - s)} u_0(l - s)ds & ; \quad t_1 < a \leq t_1 + t_2 \end{cases} \\ bv_0 e^{-\nu(t_1 + t_2 - a)} + b\displaystyle\int_0^{t_2} e^{-\nu(t_1 + t_2 - a - s)} u_0(l - s)ds \\ \quad +b\displaystyle\int_0^{t_1 - a} e^{-\nu(t_1 - a - s)} u_0(l - t_2 - s)ds \qquad ; a \leq t_1 \end{cases} \\
= & \begin{cases} u_0(a - t_1 - t_2) & ; \quad a > t_1 + t_2 \\ bv_0 e^{-\nu(t_1 + t_2 - a)} + b\displaystyle\int_0^{t_1 + t_2 - a} e^{-\nu(t_1 + t_2 - a - s)} u_0(l - s)ds & ; \quad a \leq t_1 + t_2 \end{cases} \\
= & S_1(t_1 + t_2)(u_0, v_0)(a),
\end{aligned}$$

and

$$\begin{aligned}
& S_2(t_1)S_0(t_2)(u_0, v_0) \quad = \\
= & \; v_0 e^{-\nu(t_1 + t_2)} + e^{-\nu(t_1)} \int_0^{t_2} e^{-\nu(t_2 - s)} u_0(l - s)ds + \int_0^{t_1} e^{-\nu(t_1 - s)} u_0(l - s - t_2)ds \\
= & \; v_0 e^{-\nu(t_1 + t_2)} + \int_0^{t_2} e^{-\nu(t_1 + t_2 - s)} u_0(l - s)ds + \int_{t_2}^{t_1 + t_2} e^{-\nu(t_1 + t_2 - \tau)} u_0(l - \tau)d\tau \\
= & \; v_0 e^{-\nu(t_1 + t_2)} + \int_0^{t_1 + t_2} e^{-\nu(t_1 + t_2 - s)} u_0(l - s)ds = S_2(t_1 + t_2)(u_0, v_0).
\end{aligned}$$

Then the equality (2.4) holds.
On the other hand, for h sufficiently small, we have

$$
\begin{aligned}
|S_0(h)(u_0,v_0)-(u_0,v_0)|_X &= \left|\begin{pmatrix} S_1(h)(u_0,v_0)-u_0 \\ \\ S_2(h)(u_0,v_0)-v_0 \end{pmatrix}\right|_X \\
&\leq \int_0^h \Big| bv_0 e^{-\nu(h-a)} \\
&\quad + b\int_0^{h-a} e^{-\nu(h-a-s)} u_0(l-s)ds - u_0(a)\Big| \, da \\
&\quad + \int_h^l |u_0(a-h)-u_0(a)|da + |e^{-\nu t}-1|v_0 \\
&\quad + \int_0^h e^{-\nu(h-s)}|u_0(l-s)|ds \longrightarrow 0
\end{aligned}
$$

as $h \longrightarrow 0^+$, i.e, $\lim_{h\to 0^+} S_0(h)(u_0,v_0) = (u_0,v_0)$. Furthermore $S_0(0) = I$, so the operators $\{S_0(t), 0 \leq t \leq l\}$ satisfy all the properties of a C^0-semigroup on the interval $[0,l]$.

Now we define the operators $\{S(t), t \geq 0\}$ in the form given by Lemma 2.1. The result is that this family of operators forms a C^0-semigroup.

We still have to compute the infinitesimal generator of the C^0-semigroup $\{S(t), t \geq 0\}$. So for $h > 0$ small enough, and applying theorem VIII.2 in [14] and Fubini's theorem we obtain

$$
\frac{1}{h}\left(S(h)(u_0,v_0)-(u_0,v_0)\right) = \begin{pmatrix} \frac{1}{h}\left(S_1(h)(u_0,v_0)-u_0\right) \\ \\ \frac{1}{h}\left(S_2(h)(u_0,v_0)-v_0\right) \end{pmatrix}
$$

and, assuming $u_0 \in W^{1,1}$,

$$
\begin{aligned}
\left|\tfrac{1}{h}\left(S_2(h)(u_0,v_0)-v_0\right)-u_0(l)+\nu v_0\right| &= \\
= \left|\tfrac{1}{h}\left(v_0e^{-\nu h}-v_0\right)+\nu v_0+\tfrac{1}{h}\int_0^h\left(e^{-\nu(h-s)}u_0(l-s)-u_0(l)\right)ds\right| & \\
\le \left|\tfrac{1}{h}\left(v_0e^{-\nu h}-v_0\right)+\nu v_0\right|+\left|\tfrac{1}{h}\int_0^h(u_0(l-s)-u_0(l))ds\right| &\longrightarrow 0
\end{aligned}
$$

as $h \longrightarrow 0^+$, i.e.

$$\lim_{h\to 0^+}\frac{1}{h}\left(S_2(h)(u_0,v_0)-v_0\right)=u_0(l)-\nu v_0.$$

Furthermore, a similar computation gives, in $L^1[0,l]$,

$$\lim_{h\to 0^+}\frac{1}{h}\left(S_1(h)(u_0,v_0)-u_0\right)=-\frac{du_0}{da}.$$

Indeed, using the compatibility condition, $u_0(0)=bv_0$, it follows that

$$
\begin{aligned}
&\int_0^l\left|\frac{1}{h}\left[S_1(h)(u_0,v_0)(a)-u_0(a)\right]+u_0'(a)\right|da = \\
=\ &\int_0^h\left|\frac{1}{h}\left[bv_0e^{-\nu(h-a)}+b\int_0^{h-a}e^{-\nu(h-a-s)}u_0(l-s)ds-u_0(a)\right]+u_0'(a)\right|da \\
&+\int_h^l\left|\frac{1}{h}\left[u_0(a-h)-u_0(a)\right]+u_0'(a)\right|da \\
\le\ &\tfrac{bv_0}{h}\int_0^h\left|e^{-\nu(h-a)}-1\right|da+\int_0^h\left|\frac{1}{h}\left[bv_0-u_0(a)\right]\right|da+\left|\frac{b}{h}\right|\int_0^h\int_0^{h-a}\left|u_0(l-s)\right|dsda \\
&+\int_0^h\left|u_0'(a)\right|da+\frac{1}{|h|}\int_h^l\int_{a-h}^a\left|u_0'(a)-u_0'(s)\right|dsda \\
&\le bv_0\nu h+\int_0^h\left|\frac{1}{h}\right|\int_t^h\left|u_0'(t)\right|dadt+\int_0^h\left|\frac{b}{h}\right|\left|h-s\right|\left|u_0(l-s)\right|ds\longrightarrow 0
\end{aligned}
$$

as $h \longrightarrow 0^+$. Hence, if $(u_0,v_0)\in W^{1,1}[0,l]\times \mathrm{R}$ and $u_0(0)=bv_0$ we will have

$$\lim_{h\to 0^+}\frac{1}{h}\left(S(h)(u_0,v_0)-(u_0,v_0)\right)=A\begin{pmatrix}u_0\\ v_0\end{pmatrix}.$$

On the other hand, assuming the existence of the limit of $\left(S(h)(u_0,v_0)-(u_0,v_0)\right)/h$ as $h \longrightarrow 0^+$ implies that $u_0\in W^{1,1}$ and $u_0(0)=bv_0$ (see the proof of Theorem 3.2 in

[87], p. 83 or [42], p. 535). $\square$

Remark 2.1. *Theorem 2.1 is in fact a direct consequence of a theorem due to Phillips and can be derived without computation from that theorem (see [67] or Theorem 1.2 in [4, Chap. C-II]). We chose a direct method involving explicit representation because we will use this the forthcoming.*

Let $\sigma(A)$ denote the spectrum of the operator A and $\sigma_p(A)$ be the set of its eigenvalues. The following theorem gives some properties of the spectrum of the operator A. This operator has a dominant simple real eigenvalue which represents the population growth rate.

Theorem 2.2. *A has a unique real eigenvalue λ^*, and there exists a real number $\omega < \lambda^*$ such that any other spectral value of A has a real part less than ω. Moreover, $\sigma(A) = \sigma_p(A)$.*

Proof. λ is an eigenvalue of A if there exists a nonzero vector (u, v) in the domain of A such that

$$A\begin{pmatrix} u \\ v \end{pmatrix} = \lambda \begin{pmatrix} u \\ v \end{pmatrix},$$

i.e.

$$\begin{cases} -u' &= \lambda u, \\ u(l) &= (\nu + \lambda)v, \\ u(0) &= bv. \end{cases}$$

From the first equation and the initial condition of this system, it follows that $u(a) = bve^{-\lambda a}$ and u and v are both different from 0. Hence, using the second equation,

$$b = (\nu + \lambda)e^{\lambda l} =: f(\lambda) \tag{2.5}$$

holds. Notice that $f(-\nu) = 0$ and that for $\lambda > -\nu$, f is monotonously increasing and unbounded. So there is a unique real number λ^* (which is larger than $-\nu$) such that $f(\lambda^*) = b$. On the other hand, let λ be any complex (not real) solution of (2.5). As the real part of $\nu + \lambda$ is strictly less than its modulus, we have

$$Re\lambda + \nu = Re(be^{-l\lambda}) < \left|be^{-l\lambda}\right| = be^{-lRe\lambda}$$

and therefore $f(Re\lambda) < b$ which implies $Re\lambda < \lambda^*$.

More precisely, $Re\lambda$ is bounded above by a constant, independent on λ, $\omega < \lambda^*$. Otherwise, there exists a sequence $(\lambda_n)_{n\geq 0}$ of eigenvalues of A such that $Re\lambda_n \longrightarrow \lambda^*$. But the λ_n are the zeros of an analytic function and therefore $|\lambda_n| \longrightarrow \infty$. Nevertheless, $|\lambda_n + \nu| = be^{-lRe\lambda_n} \longrightarrow be^{-l\lambda^*}$, a contradiction. Finally, it is easy to show that if λ is not an eigenvalue of A, then the operator $A - \lambda I$ is surjective then the rang of the operator $A - \lambda I$ is X and and $(A - \lambda I)^{-1}$ is continuous, hence $\sigma_p(A) = \sigma(A)$. $\Box$

The next result, which will be used when dealing with the asymptotic behaviour of the solutions of (2.1) (see Sect. 3.3.4), shows that, for the linear problem, the growth rate of the consumer population depends only on the adults population number (and on its fertility rate).

Theorem 2.3. *Let $N : X \longrightarrow \mathbb{R}$ be the bounded linear operator defined as $N(u,v) = \int_0^l u\,da + v$. Let $S(t)$ the semigroup defined in the proof of Theorem 2.1. Then $t \longrightarrow NS(t)(u_0,v_0)$ is a C^1 function of $t \geq 0$ for any $(u_0,v_0) \in X$. Moreover, $\frac{d}{dt}NS(t)(u_0,v_0) = (b-\nu)S_2(t)(u_0,v_0)$.*

Proof. In view of the semigroup property we can restrict ourselves to the case $t \in [0,l]$. So we have, using (2.3),

$$
\begin{aligned}
NS(t)(u_0,v_0) &= \int_0^t S_1(t)(u_0,v_0)(a)\,da + \int_t^l S_1(t)(u_0,v_0)(a)\,da + S_2(t)(u_0,v_0) \\
&= b\int_0^t S_2(t-a)(u_0,v_0)\,da + \int_t^l u_0(a-t)\,da + v_0e^{-\nu t} \\
&\quad + \int_0^t e^{-\nu(t-s)}u_0(l-s)\,ds \\
&= b\int_0^t S_2(t-a)(u_0,v_0)\,da + \int_0^l u_0(s)\,ds + v_0 + (e^{-\nu t}-1)v_0 \\
&\quad + \int_0^t (e^{-\nu(t-s)}-1)u_0(l-s)\,ds \\
&= b\int_0^t S_2(t-a)(u_0,v_0)\,da + N(u_0,v_0) \\
&\quad -\nu\int_0^t \left[v_0e^{-\nu s} + \int_0^s e^{-\nu(s-\sigma)}u_0(l-\sigma)\,d\sigma\right] ds \\
&= N(u_0,v_0) + (b-\nu)\int_0^t S_2(s)(u_0,v_0)\,ds,
\end{aligned}
$$

where we have used Fubini's theorem in the next to the last but one equality. Finally, the statement follows from the continuity of the integrand. □

2.4 Local existence and uniqueness

The initial value problem (2.1) does not necessarily have a solution of any kind. However, if it has a classical solution, i.e., a function $(u, v, r) \in C^1([0, \tau), X \times \mathbb{R})$ such that $(u(t), v(t)) \in D(A)$ for any $t \in [0, \tau)$ and (2.1) is satisfied on $[0, \tau)$, then it is easy, see for instance [65, Sect. 4.2], to show that this solution satisfies the following integral equation

$$\begin{pmatrix} u \\ v \\ r \end{pmatrix}(t) = T(t)\begin{pmatrix} u_0 \\ v_0 \\ r_0 \end{pmatrix} + \int_0^t T(t-s) f(u(s), v(s), r(s)) ds. \tag{2.6}$$

But in general, existence of a classical solution is not necessary to have a solution of the last equation.

Notice that, technically, it is not easy to study directly existence of a classical solution of (2.1), i.e., we cannot deal with it without using other technics. Then in order to solve System (2.1) we will use the variation of constants formula (2.6) as in [65] and we start with

Definition 2.1. *A continuous solution of the integral equation (2.6) will be called a mild solution of the initial value problem (2.2), or a mild solution of Problem (2.1).*

The following result ensures the local existence and uniqueness of mild solutions of (2.1) for a Lipschitz function f.

Theorem 2.4. *Let us assume that $m_1(a, r)$ is a locally Lipschitzian function of r, uniformly with respect to $a \in \mathbb{R}^+$, and let us assume that $m_2, g, \tilde{g}$ and h are locally Lipschitzian functions. Then, for every initial condition $w_0 = (u_0, v_0, r_0) \in Y$, there exists $0 < t_{\max}(w_0) \leq \infty$ such that Problem (2.1) has a unique mild solution (u, v, r) on the interval $[0, t_{\max})$. Moreover, if $t_{\max} < \infty$ then $\lim_{t \to t_{\max}} \sup |w(t)|_Y = \infty$.*

Proof. It suffices to prove that the function f is locally Lipschitzian on Y, which implies the proof according to the theory of semilinear equations (see Theorem 1.4 in [65, Chap. 6]).

Let $m_1, m_2, g, \tilde{g}$ and h be respectively $M_1, M_2, G, \tilde{G}$ and H Lipschitzian. Let then (u_1, v_1, r_1) and (u_2, v_2, r_2) belong to the Banach space Y such that $|(u_1, v_1, r_1)|_Y \leq R_0$ and $|(u_2, v_2, r_2)|_Y \leq R_0$ for some constant $R_0 \in \mathbb{R}$. Therefore there exists a real number $C > 0$ such that $|f(u_1, v_1, r_1)|_Y \leq C$ and $|f(u_2, v_2, r_2)|_Y \leq C$. So we have

$$\begin{aligned} |f(u_1, v_1, r_1) - f(u_2, v_2, r_2)|_Y \leq\ & |m_1(a, r_1)u_1 - m_1(a, r_2)u_2|_{L^1[0,l]} \\ & + |m_2(r_1)v_1 - m_2(r_2)v_2| \\ & + |g(r_1)r_1 - g(r_2)r_2| \\ & + |h(L(u_1, v_1))\tilde{g}(r_1) - h(L(u_2, v_2))\tilde{g}(r_2)|. \end{aligned}$$

On the other hand, it follows that

$$\begin{aligned} |m_1(a, r_1)u_1 - m_1(a, r_2)u_2|_{L^1[0,l]} &= |m_1(a, r_1)[u_1 - u_2] \\ &\quad + [m_1(a, r_1) - m_1(a, r_2)]u_2|_{L^1[0,l]} \\ &\leq |m_1(a, r_1)||u_1 - u_2|_{L^1[0,l]} + M_1 R_0 |r_1 - r_2| \\ &\leq C|u_1 - u_2|_{L^1[0,l]} + M_1 R_0 |r_1 - r_2|, \end{aligned}$$

$$\begin{aligned} |m_2(r_1)v_1 - m_2(r_2)v_2| &= |m_2(r_1)[v_1 - v_2] + [m_2(r_1) - m_2(r_2)]v_2| \\ &\leq |m_2(r_1)||v_1 - v_2| + M_2 R_0 |r_1 - r_2| \\ &\leq C|v_1 - v_2| + M_2 R_0 |r_1 - r_2|, \end{aligned}$$

$$\begin{aligned} |g(r_1)r_1 - g(r_2)r_2| &= |g(r_1)[r_1 - r_2] + [g(r_1) - g(r_2)]r_2| \\ &\leq |g(r_1)||r_1 - r_2| + G R_0 |r_1 - r_2| \end{aligned}$$

and

$$\begin{aligned} |h(L(u_1, v_1))\tilde{g}(r_1) - h(L(u_2, v_2))\tilde{g}(r_2)| &= |h(L(u_1, v_1))[\tilde{g}(r_1) - \tilde{g}(r_2)] \\ &\quad + [h(L(u_1, v_1)) - h(L(u_2, v_2))]\tilde{g}(r_2)| \\ &\leq C\tilde{G}|r_1 - r_2| \\ &\quad + H R_0 ||L|| \left(|u_1 - u_2|_{L^1[0,l]} + |v_1 - v_2|\right). \end{aligned}$$

Finally, we have

$$\begin{aligned} & |f(u_1, v_1, r_1) - f(u_2, v_2, r_2)|_Y \leq \\ \leq\ & \Big(C(1 + \tilde{G}) + R_0(M_1 + M_2 + G)\Big) |r_1 - r_2| + (C + H R_0 ||L||)|v_1 - v_2| \\ & + (C + H R_0 ||L||)|u_1 - u_2|_{L^1[0,l]} \\ \leq\ & \max\Big(C(1 + \tilde{G}) + R_0(M_1 + M_2 + G), C + H R_0 ||L||\Big) |(u_1, u_1, r_1) - (u_2, v_2, r_2)|_Y. \end{aligned}$$

2.5 Continuous dependence on initial age distributions

After we have shown that the initial value problem (2.1) has a unique local mild solution, the goal of this subsection is to show that the local solutions depend continuously on the initial age distributions. That is, given two close initial conditions, the corresponding mild solutions remain close to each other.

Notice also that a similar proof of the following proposition can be found in the proof of [40, Theorem 3.4.1] for the analytic semigroup case.

Proposition 2.1. *Let $w_0 \in Y$. For any $t_1 \in [0, t_{\max}(w_0))$ and for any $\varepsilon > 0$ there exists $\delta > 0$ such that if $|\tilde{w}_0 - w_0|_Y < \delta$ then $t_{\max}(\tilde{w}_0) > t_1$ and $|\tilde{w}(t) - w(t)|_Y < \varepsilon$ for $t \in [0, t_1]$ where $w(t)$ and $\tilde{w}(t)$ are the two local mild solutions of Problem (2.1) corresponding respectively to initial conditions w_0 and $\tilde{w}_0$.*

Proof. Let R be a real number such that $|w(t) - w_0|_Y < \frac{R}{2}$ for $t \in [0, t_1]$ and let $\tilde{L} := \tilde{L}(w_0, R)$ be such that $|f(w_1) - f(w_2)| < \tilde{L}|w_1 - w_2|_Y$ whenever $|w_i - w_0|_Y < R, i = 1, 2$.

Let us assume that $|\tilde{w}_0 - w_0|_Y < R$. Let us recall the bound $\|T(t)\| \leq Me^{\omega t}$. First, we shall prove that if $|\tilde{w}_0 - w_0|_Y$ is sufficiently small, explicitly if $|\tilde{w}_0 - w_0|_Y < \frac{R}{4M}e^{-kt_1}$ where $k := \max(\tilde{L}M + \omega, 0)$, then $|\tilde{w}(s) - w_0|_Y < R$ for $0 \leq s \leq t_1$. Otherwise, let us assume that the claim does not hold and let $t_0 = \inf_{s \in [0,t_1]}\{s : |\tilde{w}(s) - w_0|_Y \geq R\}$. So $|\tilde{w}(s) - w_0|_Y < R$ for $0 \leq s < t_0$ and $|\tilde{w}(t_0) - w_0|_Y = R$ by continuity.

From the integral equations

$$w(t) = T(t)w_0 + \int_0^t T(t-s)f(w(s))ds$$

and

$$\tilde{w}(t) = T(t)\tilde{w}_0 + \int_0^t T(t-s)f(\tilde{w}(s))ds,$$

we will have

$$|w(t) - \tilde{w}(t)|_Y \leq Me^{\omega t}|w_0 - \tilde{w}_0|_Y + M\tilde{L}\int_0^t e^{\omega(t-s)}|w(s) - \tilde{w}(s)|_Y ds$$

for $0 \leq t < t_0$. By Gronwall's inequality it readily follows that

$$|w(t) - \tilde{w}(t)|_Y \leq Me^{(\tilde{L}M+\omega)t}|w_0 - \tilde{w}_0|_Y \leq Me^{kt_1}|w_0 - \tilde{w}_0|_Y < \frac{R}{4} \tag{2.7}$$

and therefore,

$$|\tilde{w}(t) - w_0|_Y \leq |\tilde{w}(t) - w(t)|_Y + |w(t) - w_0|_Y < \frac{3}{4}R$$

for $t \leq t_0$, a contradiction.

Moreover, (2.7) holds whenever $|\tilde{w}(t) - w_0|_Y < R$, i.e. for $t \in [0, t_1]$. So the statement of this proposition follows with $\delta = \min(\frac{R}{4}, \varepsilon)\frac{e^{-kt_1}}{M}$. $\square$

2.6 Positivity of solutions and global existence

The first aim of this subsection is to study the positivity of the solutions in order the initial value problem to have a biological sense. We start with the positivity also because this is a necessary condition to have global existence.

Theorem 2.5. *If the initial condition $w_0 := (u_0, v_0, r_0) \in Y$ is positive then the mild solution (u, v, r) of Problem (2.1) defined on $[0, t_{\max}(w_0))$ is also positive.*

Proof. First notice that if r_0 is strictly positive then $r(t)$ cannot become negative. Indeed, if there exists some T such that $r(T) = 0$ then $r(t)$ is a solution of the following ordinary differential equation

$$\begin{cases} r' &= (g(r) - \tilde{h}(t))r \\ r(T) &= 0, \end{cases}$$

where $\tilde{h}(t) := h(L(u(t), v(t)))$. As the function $\tilde{r}(t) \equiv 0$ is also a solution of this problem, this contradicts the uniqueness of solution of the initial value problem for ordinary differential equations.

Let us add and subtract κu and κv, where κ is a constant larger than the two functions $m_1(a, r)$ and $m_2(r)$, respectively to the right hand side of the first and the second equations of Problem (2.1). We can think of these two first equations as a semilinear nonautonomous equation (here $r(t)$ is a given function of t) with a uniformly Lipschitz continuous nonlinearity. From the proof of Theorem 1.2 of [65, Chap.6] it follows that the mild solution $(u(t), v(t))$ is the limit, on $[0, T]$ for all $T < t_{\max(w_0)}$, of the sequence $(u_n(t), v_n(t))_{n\geq 0}$ where (u_n, v_n) is given by

$$\begin{pmatrix} u_{n+1} \\ v_{n+1} \end{pmatrix}(t) = S_\kappa(t)\begin{pmatrix} u_0 \\ v_0 \end{pmatrix} + \int_0^t S_\kappa(t-s)\begin{pmatrix} (\kappa - m_1(a, r(s)))u_n(s) \\ (\kappa - m_2(r(s)))v_n(s) \end{pmatrix} ds$$

and where $S_\kappa(t) := e^{-\kappa t}S(t)$ is the semigroup generated by the operator $(A - \kappa I)$. Now, using the positivity of the semigroup $S_\kappa(t)$ and the positivity of the two functions $\kappa - m_1(a, r)$ and $\kappa - m_2(r)$ and induction on n it readily follows that the sequence $(u_n, v_n)_{n\geq 0}$ is positive in the Banach space X whenever the initial condition (u_0, v_0) is positive. Therefore, its limit (u, v) is also in the positive cone of X. $\square$

In general a global Lipschitz condition on the nonlinearities ensures the existence of global mild solutions of (2.1). But the next theorem shows, assuming only a local Lipschitz condition on the functions $m_1, m_2, g, \tilde{g}$ and h, the global existence of mild solutions which will automatically be positive if the initial condition belongs to the positive cone of the state space Y.

Theorem 2.6. *Let us assume the same hypotheses as in Theorem 2.4. For any positive initial condition in Y, the initial value problem (2.1) has a unique mild solution in the whole interval* $[0, \infty)$.

Proof. From Theorem 2.4 there exists some $t_{\max} > 0$ such that Problem (2.1) has a unique mild solution (u, v, r) on the interval $[0, t_{\max})$ corresponding to the initial condition (u_0, v_0, r_0). So, in order to show the statement of the theorem, it suffices (see Theorem 1.4 in [65, Chap. 6]) to prove that $t_{\max} < \infty$ implies $\lim_{t\to t_{\max}} \sup |(u(t), v(t), r(t))|_Y < \infty$. As $r'(t)$ is negative for $r > r_c$, it is clear that $r(t)$ is bounded above and it is bounded below by 0 by Theorem 2.5. As above let us denote by κ an upper bound of $m_1(a, r)$ and $m_2(r)$ and notice that $\|S(t)\| \leq Me^{\omega t}$. We have, for every $t \in [0, t_{\max})$,

$$\begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = S(t)\begin{pmatrix} u_0 \\ v_0 \end{pmatrix} - \int_0^t S(t-s)\begin{pmatrix} m_1(a, r(s))u(s) \\ m_2(r(s))v(s) \end{pmatrix} ds, \tag{2.8}$$

so

$$|(u(t), v(t))|_X \leq Me^{\omega t}|(u_0, v_0)|_X + M\kappa e^{\omega t} \int_0^t e^{-\omega s}|(u(s), v(s))|_X ds,$$

i.e.,

$$|(u(t), v(t))|_X e^{-\omega t} \leq M|(u_0, v_0)|_X + M\kappa \int_0^t e^{-\omega s}|(u(s), v(s))|_X ds.$$

Applying Gronwall's inequality, it follows from the last inequality that

$$|(u(t), v(t))|_X \leq M|(u_0, v_0)|_X e^{(\omega+M\kappa)t}$$

and therefore if $t_{\max} < \infty$ then

$$\lim_{t \to t_{\max}} \sup |u(t), v(t), r(t)|_Y < \infty. \ \Box$$

Remark 2.2. *Initial conditions belonging to the domain of B and smoothness of the nonlinear functions m_1, m_2, g and h imply that the mild solution of Problem (2.1) is a classical one (see Theorem 1.5 in [65, Chap.6]).*

2.7 Existence of equilibrium solutions

To end this chapter we study in this section the equilibrium solutions belonging to the positive cone of Y. The following results will be used when dealing with the study of the asymptotic behaviour of solutions of the initial value problem (2.1).

Theorem 2.7. *If $b \in \left[0, m_2(r_c)e^{\int_0^l m_1(a,r_c)\,da}\right]$ or $b > m_2(0)e^{\int_0^l m_1(a,0)\,da}$, the only equilibrium points of System (2.1) are $(0,0,0)$ and $(0,0,r_c)$.*

If $b \in \left(m_2(r_c)e^{\int_0^l m_1(a,r_c)\,da}, m_2(0)e^{\int_0^l m_1(a,0)\,da}\right)$ then there exists also a unique co-existence equilibrium point (u_e, v_e, r_e). Moreover $0 < r_e < r_c$.

Finally, if $b = m_2(0)e^{\int_0^l m_1(a,0)\,da}$ the equilibria are $(0,0,0), (0,0,r_c)$ and, for any $v > 0$, $\left(bve^{-\int_0^a m_1(a',0)\,da'}, v, 0\right)$.

Proof. The equilibrium points are the solutions of the following system:

$$\begin{cases} u'(a) + m_1(a,r)u(a) &= 0, \\ u(l) - m_2(r)v &= 0, \\ [g(r) - h(L(u,v))]\,r &= 0, \\ u(0) - bv &= 0. \end{cases} \tag{2.9}$$

First notice that the first and last equations are equivalent to having

$$u(a) = bve^{-\int_0^a m_1(a',r)\,da'}.$$

So if $v = 0$ then $u \equiv 0$ and $g(r)r = 0$, that is, $r = 0$ or $r = r_c$. Then $(0,0,0)$ and $(0,0,r_c)$ are the only equilibrium solutions with $v = 0$. Otherwise, i.e. if $v \neq 0$, the second equation reduces to $b = m_2(r)e^{\int_0^l m_1(a,r)\,da}$.

As the functions m_1 and m_2 are strictly decreasing with respect to the amount of resources, then the function $r \longrightarrow m_2(r)e^{\int_0^l m_1(a,r)\,da}$ is strictly decreasing too. So, in the assumption of the first statement, there exists no solution r of $b = m_2(r)e^{\int_0^l m_1(a,r)\,da}$ smaller than r_c. Then, by the third equation, there is no equilibrium with $v > 0$.

If $b \in \left(m_2(r_c)e^{\int_0^l m_1(a,r_c)\,da}, m_2(0)e^{\int_0^l m_1(a,0)\,da}\right)$, there exists a unique $r_e \in (0, r_c)$ such that $b = m_2(r_e)e^{\int_0^l m_1(a,r_e)\,da}$. On the other hand, as h is a strictly increasing unbounded function vanishing at 0 then there exists a unique v_e such that $u_e(a) = bv_e e^{-\int_0^l m_1(a,r_e)\,da}$ and $g(r_e) = h(L(u_e, v_e))$. That is, (u_e, v_e, r_e) is the only coexistence equilibrium solution.

In the third assumption, $r = 0$ solves the second and the third equations and so the statement follows. $\square$

Chapter 3

Asymptotic Behaviour in the Uniform Increase of Mortality Case

3.1 Introduction

In this chapter we find out the asymptotic behaviour of System (2.1) in the case of uniform increase of mortality, i.e. when the death rates of juveniles and adults differ by a constant: $m_2(r) = \nu + m_1(r)$. That is, both consumer populations react in the same way to the amount of resources. This allows to write (2.1) in an abstract form in such a way that the infinite dimensional part of it (the equations for u and v) take the form:

$$x' = Ax - m(r)x.$$

This permits a reduction to a nonautonomous two dimensional system, which in its turn is studied analyzing its limit system by classical methods (using Theorem 3.7, Theorem 3.8 and Theorem 3.9).

The results depend on the number λ^* which is the dominant eigenvalue of the operator A (see Theorem 2.2). In other words, the dynamics of (2.1) depends on the fertility of the adults b since λ^* is the only solution of the equation $b = (\nu + \lambda^*)e^{\lambda^* l}$ (see the proof of Theorem 2.2).

In the case where $\tilde{g}(r) = r$ we will determine completely the dynamics of our system and we will show the existence of an attractor, but in the case where $\tilde{g}(r)$ is any increasing C^1−function globally bounded from above (to take into account the "satiation" of the consumers), the asymptotic behaviour of (2.1) is complicated and the existence of a global attractor requires more conditions.

Let us now assume $m_1(r) = \nu_1 + \overline{m}(r)$ and $m_2(r) = \nu_2 + \overline{m}(r)$ where ν_1 and ν_2 are two constants. Denote $m(r) := \nu_1 + \overline{m}(r)$ and $\nu := \nu_2 - \nu_1$. Then $m_2(r) = \nu + m(r)$. Consequently, we can write system (2.1) in the following abstract form:

$$\begin{cases} \begin{pmatrix} u \\ v \end{pmatrix}' & = & A \begin{pmatrix} u \\ v \end{pmatrix} - m(r) \begin{pmatrix} u \\ v \end{pmatrix}, \\ r' & = & g(r)r - h(L(u,v))\tilde{g}(r), \\ u(.,0) & = & u_0(.), \quad v(0) = v_0, \quad r(0) = r_0, \end{cases} \tag{3.1}$$

where the operator

$$A := \begin{pmatrix} -\frac{d}{da} & 0 \\ & \\ E_l & -\nu \end{pmatrix}$$

is defined in the previous chapter.

3.2 Reduction to a nonautonomous ordinary differential system

In order to deal with this section, firstly we will use a technique based on the translation of the eigenvalues of the operator A to the left so that 0 will be an eigenvalue of another operator $\tilde{A}$ which will generate the C^0-semigroup $\left\{\tilde{S}(t), t \geq 0\right\}$ such that

$$\tilde{S}(t) := e^{-\lambda^* t} S(t).$$

Thus, we will prove using the method of "variation of constants" that in the case of uniform increase mortality the mild solutions (or the classical solutions) have the following form

$$\left(\psi(t)\tilde{S}(t)(u_0, v_0), r(t)\right),$$

where ψ is a real function. So, this will result in a nonautonomous system of two ordinary differential equations.

Adding and subtracting $\lambda^*\binom{u}{v}$ to the second member of the first equation of (3.1), the initial value problem becomes:

$$\begin{cases} \begin{pmatrix} u \\ v \end{pmatrix}' & = & \tilde{A}\begin{pmatrix} u \\ v \end{pmatrix} - (m(r)-\lambda^*)\begin{pmatrix} u \\ v \end{pmatrix}, \\ r' & = & g(r)r - h(L(u,v))\tilde{g}(r), \\ u(a,0) & = & u_0(a), \quad v(0) = v_0, \quad r(0) = r_0, \end{cases} \tag{3.2}$$

where

$$\tilde{A} := \begin{pmatrix} -\frac{d}{da} - \lambda^* & 0 \\ & \\ E_l & -\nu - \lambda^* \end{pmatrix}$$

is an operator in the Banach space X with $D(\tilde{A}) = D(A)$.

Theorem 3.1. *The operator $\tilde{A}$ is the infinitesimal generator of the C^0-semigroup $\{\tilde{S}(t),\, t \geq 0\}$.*

Proof. Notice that in order to prove this statement it suffices to show that if $(u,v) \in D(A)$ satisfies

$$\begin{cases} \binom{u}{v}' & = & A\binom{u}{v} \\ u(0,t) & = & bv(t) \end{cases} \tag{3.3}$$

then, $e^{-\lambda^* t}(u,v)$ is the solution of the following system

$$\begin{cases} \binom{u}{v}' & = & \tilde{A}\binom{u}{v} \\ u(0,t) & = & bv(t). \end{cases} \tag{3.4}$$

Let then $w = e^{-\lambda^* t} u$ and $z = e^{-\lambda^* t} v$, therefore

$$\begin{aligned}
\begin{pmatrix} w \\ z \end{pmatrix}' &= \begin{pmatrix} -\lambda^* e^{-\lambda^* t} u + e^{-\lambda^* t} u' \\ \\ -\lambda^* e^{-\lambda^* t} v + e^{-\lambda^* t} v' \end{pmatrix} \\
&= \begin{pmatrix} -\lambda^* e^{-\lambda^* t} u - e^{\lambda^* t} \frac{du}{da} \\ \\ -\lambda^* e^{-\lambda^* t} v + e^{-\lambda^* t} u(l,t) \end{pmatrix} \\
&= \begin{pmatrix} \left(-\frac{d}{da} - \lambda^*\right) w \\ \\ E_l w - \lambda^* z \end{pmatrix} \\
&= \tilde{A} \begin{pmatrix} w \\ z \end{pmatrix}.
\end{aligned}$$

On the other hand we have

$$\begin{aligned}
w(0,t) &= e^{-\lambda^* t} u(0,t) \\
&= e^{-\lambda^* t} b v(t) \\
&= bz.
\end{aligned}$$

Then the statement holds. $\square$

Considering now the function

$$t \longrightarrow \psi(t) \tilde{S}(t)(u_0, v_0)$$

for fixed (u_0, v_0) belonging to the domain of $\tilde{A}$, and substituting it into the equation $(3.2)_1$, we obtain

$$\psi' \tilde{S}(t) \binom{u_0}{v_0} + \psi \tilde{A} \tilde{S}(t) \binom{u_0}{v_0} = \psi \tilde{A} \tilde{S}(t) \binom{u_0}{v_0} - (m(r) - \lambda^*) \psi \tilde{S}(t) \binom{u_0}{v_0},$$

which implies that

$$\psi' = (\lambda^* - m(r))\,\psi$$

with $\psi(0) = 1$. Therefore, we get the following nonautonomous ordinary differential system

$$\begin{cases} r' &= g(r)r - h\left(L\left(\psi\tilde{S}(t)(u_0, v_0)\right)\right)\tilde{g}(r), \\ \psi' &= (\lambda^* - m(r))\psi, \end{cases} \tag{3.5}$$

supplemented with the initial condition. Next, we consider this system with the initial condition $(u_0, v_0) \in X$. We will show that the nonautonomous ordinary differential system (3.5) has a unique positive solution if $(u_0, v_0, r_0) \in Y^+$.

So, let $F : [0, \infty) \times \mathbb{R}^2 \longrightarrow \mathbb{R}^2$ be the function defined by

$$F(t, (r, \psi)) := \begin{pmatrix} g(r)r - \tilde{h}(t, \psi)\tilde{g}(r) \\ (\lambda^* - m(r))\,\psi \end{pmatrix}$$

where

$$\tilde{h}(t, \psi) := h\left(L\left(\psi\tilde{S}(t)\begin{pmatrix} u_0 \\ v_0 \end{pmatrix}\right)\right).$$

Lemma 3.1. *If $m, g, \tilde{g}$ and h are locally Lipschitzian functions then the function F is also locally Lipschitzian in (r, ψ), uniformly in t on bounded intervals.*

Proof. Firstly, it is easy to see that the function $\tilde{h}$ is locally Lipschitzian uniformly on bounded intervals (with constant $\tilde{H}$) because the function h is locally Lipschitzian. Let R be any positive number and let M, G and $\tilde{G}$ be the Lipschitz constants of m, g and $\tilde{g}$ in the closed ball of center the origin and radius R of $\mathbb{R}^2$. There exists a positive number K such that $g(r), \tilde{g}(r), m(r)$ and $\tilde{h}(t, \psi)$ are small than K if $|(r, \psi)| \leq R$. So we get for $|(r_1, \psi_1)| \leq R$ and $|(r_2, \psi_2)| \leq R$,

$$\begin{aligned} &|F(t, (r_1, \psi_1)) - F(t, (r_2, \psi_2))|_{\mathbb{R}^2} = \\ = \;& \left|\begin{pmatrix} g(r_1)r_1 - \tilde{h}(t, \psi_1)\tilde{g}(r_1) - g(r_2)r_2 - \tilde{h}(t, \psi_2)g(r_2) \\ (\lambda^* - m(r_1))\,\psi_1 - (\lambda^* - m(r_2))\,\psi_2 \end{pmatrix}\right|_{\mathbb{R}^2} \\ = \;& \left|g(r_1)r_1 - \tilde{h}(t, \psi_1)\tilde{g}(r_1) - g(r_2)r_2 - \tilde{h}(t, \psi_2)\tilde{g}(r_2)\right| \\ & + |(\lambda^* - m(r_1))\,\psi_1 - (\lambda^* - m(r_2))\,\psi_2|\,. \end{aligned}$$

After it follows that

$$\begin{aligned}
& \left|g(r_1)r_1 - \tilde{h}(t,\psi_1)\tilde{g}(r_1) - g(r_2)r_2 - \tilde{h}(t,\psi_2)\tilde{g}(r_2)\right| \le \\
\le\ & |g(r_1)r_1 - g(r_2)r_2| + \left|\tilde{h}(t,\psi_1)\tilde{g}(r_1) - \tilde{h}(t,\psi_2)\tilde{g}(r_2)\right| \\
=\ & |(g(r_1) - g(r_2))\, r_1 + g(r_2)(r_1 - r_2)| \\
& + \left|\left(\tilde{h}(t,\psi_1) - \tilde{h}(t,\psi_2)\right)\tilde{g}(r_1) + \tilde{h}(t,\psi_2)\left(\tilde{g}(r_1) - \tilde{g}(r_2)\right)\right| \\
\le\ & GR\,|r_1 - r_2| + K\,|r_1 - r_2| + \tilde{H}K\,|\psi_1 - \psi_2| + K\tilde{G}\,|r_1 - r_2| \\
=\ & (GR + K + K\tilde{G})\,|r_1 - r_2| + \tilde{H}K\,|\psi_1 - \psi_2)|\,.
\end{aligned}$$

on the other hand we have

$$\begin{aligned}
|(\lambda^* - m(r_1))\psi_1 - (\lambda^* - m(r_2))\psi_2| &= |\lambda^*(\psi_1 - \psi_2) \\
&\quad -(m(r_1) - m(r_2))\psi_1 - m(r_2)(\psi_1 - \psi_2)| \\
&\le (\lambda^* + K)|\psi_1 - \psi_2| + MR|r_1 - r_2|.
\end{aligned}$$

Finally

$$|F(t,(r_1,\psi_1)) - F(t,(r_2,\psi_2))| \le C|r_1,\psi_1) - (r_2,\psi_2)|_{\mathbb{R}^2}$$

where $C := \max(GR + K + K\tilde{G} + MR\ ,\ \tilde{H}K + \lambda^* + K)$. Therefore, F is locally Lipschitzian. $\square$

Theorem 3.2. *For any $(u_0, v_0, r_0) \in Y^+$, if $m, g, \tilde{g}$ and h are locally Lipschitzian functions then the ordinary differential system (3.5) has a unique global solution $(r(t), \psi(t))$.*

Proof. First, from the previous lemma the function F is a locally Lipschitz continuous function, so that there exists $t_{\max} > 0$ such that system (3.5) has a unique solution (r, ψ) on the interval $[0, t_{\max})$. If furthermore, $t_{\max} < \infty$, then $\lim_{t \to t_{max}} \sup |(r,\psi)|_{\mathbb{R}^2} = \infty$. But it is clear that the function $r(t)$ is bounded above since the function g is negative from r_c onward and furthermore we have

$$\psi(t) = e^{\lambda^* t - \int_0^t m(r(s))ds}.$$

So $\sup |(r,\psi)|$ does not tend to infinite as t tends to $t_{\max} < \infty$. From this, it follows that $t_{max} = \infty$. $\square$

Proposition 3.1. *If $(u_0, v_0, r_0) \in Y^+$ then the solution $(r(t), \psi(t))$ of the ordinary differential system (3.5) is positive.*

Proof. Firstly, from the proof of the previous theorem it is clear that the function ψ is always positive. On the other hand the positivity of the function r was proved in the proof of Theorem 2.5. $\square$

Theorem 3.3. *For any $(u_0, v_0, r_0) \in Y^+$, let $(r(t), \psi(t))$ be the global solution of the ordinary differential system (3.5). Then the initial value problem (3.1) has a unique positive global mild solution which is of the form*

$$\left(\psi(t)\tilde{S}(t)(u_0, v_0), r(t)\right).$$

Furthermore, it is classical if (u_0, v_0) is in the domain of the operator A.

Proof. In order to prove this result it suffices to show that $\psi(t)\tilde{S}(t)(u_0, v_0)$ is the mild solution of the first equation of (3.2). On the other hand notice that the function ψ satisfies

$$\psi(t) = 1 + \int_0^t (\lambda^* - m(r(s)))\psi(s)\, ds.$$

So it follows that

$$\begin{aligned}
& \tilde{S}(t)(u_0, v_0) + \int_0^t \tilde{S}(t-s)(\lambda^* - m(r(s)))\psi(s)\tilde{S}(s)(u_0, v_0)\, ds = \\
= \ & \tilde{S}(t)(u_0, v_0) + \int_0^t (\lambda^* - m(r(s)))\psi(s)\tilde{S}(t-s)\tilde{S}(s)(u_0, v_0)\, ds \\
= \ & \tilde{S}(t)(u_0, v_0) + \int_0^t (\lambda^* - m(r(s)))\psi(s)\tilde{S}(t)(u_0, v_0)\, ds \\
= \ & \left(1 + \int_0^t (\lambda^* - m(r(s)))\psi(s)\, ds\right) \tilde{S}(t)(u_0, v_0) \\
= \ & \psi(t)\tilde{S}(t)(u_0, v_0). \square
\end{aligned}$$

Remark 3.1. *Notice that, for the initial value problem (3.1) global existence, uniqueness and positivity of the solution had been already proved in the previous chapter, using the theory of a semilinear equation (see Sect. 2.4 and Sect. 2.6). The advantage of proof undertaken in Theorem 3.3 is that in the case of the uniform increase of mortality, we prove that the solution of (3.1) can be written in the following form*

$$(u(t), v(t), r(t)) = (\psi(t)\tilde{S}(t)(u_0, v_0), r(t))$$

which permits to determine completely the dynamics of (3.1) in some cases. We also note that in this special case uniqueness can be proved separately as in [15] and a similar proof, in a slightly different case, can be found in [17].