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Evolution of Sex-ratio in Structured Population Dynamics

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Certifico que la present memòria ha estat realitzada per Jordi Ripoll i Missé i dirigida per mi.

Girona, juny de 2005

Dr. Àngel Calsina i Ballesta

*“To my wife Elisabet, with love,
and to our child Aleix”*

“SEBBENE di un interesse di giorno in giorno crescente le applicazioni delle matematiche alle scienze biologiche ci appaiono esse pure al loro inizio”. *Vito Volterra at the opening lecture in Rome on the year 1901.*

“AS many more individuals of each species are born than can possibly survive, and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected”. *Charles Darwin, The Origin of Species, 1859.*

“ADMETEU, dintre el soroll, si us plau, que la cultura –la intel·lectual, d’una manera preferent– és *interpretació de la vida*, vàlida en un moment determinat de la vida, ara i aquí, encara que em desagrada fins al mareig aquest lloc comú. Interpretació a l’altura del temps en què ens toca de viure, tenint molt en compte el passat, però esguardant-lo no com l’ocell al serpent, amb una fascinació paralítica, sinó procurant sense treva de superar-lo”. *Salvador Espriu, Universitat de Barcelona, 1980.*

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Tatilibisness

Avui és un gran dia. Permeteu-me que escrigui aquests agraïments/reflexions en una sola tarda, com si es tractés d'un article periodístic que hagués de sortir en l'edició de demà d'algun diari imaginari (e.g. $\sqrt{-1}$), d'una manera semblant a com vaig escriure l'article titulat *Tatilibisness* publicat a la revista *Aleph*. Suposo que us deueu estar preguntant pel significat d'aquesta paraula!? En aquells moments jo cursava el primer curs a la Facultat de Matemàtiques de la Universitat de Barcelona i l'*Aleph* era la revista-magazine de la facultat. Jo escrivia *pel plaer d'escriure*, sense cap altra intenció. Permeteu-me doncs que recuperi, ni que sigui breument, aquell plaer intel·lectual. El fet que ho vulgui escriure en unes poques hores és simplement perquè aquestes reflexions les tinc ja molt pensades (de fa anys fins i tot!), són com uns pensaments que s'han quedat en 'stand by' rondant pel meu cap i que ara voldria foragitar. M'agradaria cridar i que el lector pogués sentir el crit que expressa l'emoció de poder escriure finalment aquestes breus ratlles, que tanquen un llarg procés que un dia, sense saber ben bé com, vaig començar sol·lícitament amb tota la innocència d'aquest món.

Ja que una tesi no deixa de ser quelcom que un fa per a un mateix, deixeu-me doncs que parli una mica de mi, tot fent un repàs a l'estructura en edat (*etapes vitals*) de l'espècie humana, cosa que de passada introdueix el lector en la temàtica d'aquest treball: l'estudi de poblacions amb estructura en edat.

De ben petit (etapa de la infantesa) el que més m'agradava era dibuixar i pintar, tenia el que podríem dir inquietuds plàstiques, em passava hores dibuixant, es podria dir que era un nen 'tranquil', pacient i assossegat. Posteriorment (inici de l'etapa de l'adolescència) en l'edat del *pavo*, les meves inquietuds van girar a l'entorn de la música (*l'aliment de l'esperit*), el solfeig, la guitarra i fins i tot un grup musical que vam formar amb la colla d'amics de Canet. A les acaballes de l'etapa adolescent, la meva passió va ser escriure, com he dit abans, escriure pel plaer d'escriure. Va ser poc abans de començar els meus estudis universitaris. Per un noi de poble com jo, anar a estudiar a Barcelona va ser com *sortir de l'ou*, com fer-se gran, és a dir, iniciar l'etapa de l'adultesa/maduresa. A la facultat parlàvem de l'actualitat, de política, de catalanisme, de ciència en general. Com no podia ser de cap altra manera, ens fèiem un fart d'estudiar, però valia la pena, va ser una experiència genial! En referència a les meves experiències vitals anteriors, suposo que les matemàtiques em devien semblar una 'manera' de poder seguir "dibuixant" i "escrivint". Per mi un matemàtic és una persona que té una *sensibilitat* especial. Al cap i la fi, la ciència (les matemàtiques sobretot) és una de les poques coses en què tots els sers humans ens podem posar d'acord.

Un cop acabada la carrera i després de treballar com a programador informàtic durant un any vaig començar els estudis de doctorat, corria l'any 96. Inicialment em vaig interessar per la mecànica celeste (dimensió finita i molt no-lineal), però per circumstàncies de la vida em vaig canviar a la dinàmica de poblacions estructurades (dimensió infinita i poc no-lineal). Com diu l'Àngel, el meu director de tesi, si un sistema ha de tenir dimensió més gran que dos, gairebé prefereixo que sigui de dimensió infinita. I ara, en aquests precisos moments que acabo de ser pare (etapa de la maduresa pròpiament dita) és quan presento (per fi) aquesta tesi.

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Jordi.

In memoriam: Enriqueta Masvidal i Dalmau (1909–2002)†.

Chapter 1

Introduction

MATHEMATICAL modelling has its own place in all sciences. The thesis that you are holding in your hands concerns mathematical models in the biological sciences, or rather a very small area called *structured population dynamics*. This subject matter, as its name suggests, is about the evolution in time of biological populations (animals, cells ...) or sometimes human populations, with an *internal structure* given by one or several variables which are generally physiological characteristics. Actually, this structure allow us to incorporate the *diversity* of the individuals of the population into the models. So, the individuals of the population are distinguished by these structuring variables like age, body size, protein content, sex, cell maturity, phenotype, position in space (external structure), or any other trait/factor with a significant effect on (maturation), survival and reproduction.

Whenever the phenomenon we are interested in is related to the diversity that can be exhibited by the individuals constituting a population, the structured population dynamics approach/perspective turns out to be suitable.

The topic stems from simple deterministic (unstructured) models of population dynamics for a single-species as the Malthus equation and the *generalized* Verhulst equation (a Bernoulli equation). In continuous time, these basic models take the form of an ordinary differential equation for the population size (total population) and some of them can be explicitly solved by simple methods of integration, like separation of variables.

Here, we give a brief discussion of these two elementary but fundamental examples. The Malthus equation predicts *exponential* population growth. Indeed, considering a closed population, e.g. a single species living isolated, and calling $N(t)$ to the size of the population at time t ,

one has that

$$N'(t) = r(t) N(t), \quad r(t) \text{ is the intrinsic growth rate,} \quad N(t) = N(t_0) e^{\int_{t_0}^t r(s) ds}.$$

The term $r(t)$ is related to the birth and death processes. On the other hand, the Bernoulli equation predicts *logistic* population growth, that is, monotonic convergence to a non-trivial equilibrium state. Indeed, the previous linear equation is modified into the following non-linear one:

$$N'(t) = r(t) \left(1 - \left(\frac{N(t)}{K}\right)^\theta\right) N(t), \quad K > 0 \text{ is the carrying capacity, } \theta > 0,$$

and making a change of variables ¹:

$$x = N^\theta, \quad \frac{dx}{dt} = \theta N^{\theta-1} \frac{dN}{dt}, \quad x(t) = \frac{K^\theta x(t_0)}{x(t_0) + (K^\theta - x(t_0)) e^{-\theta \int_{t_0}^t r(s) ds}}, \quad N(t) = (x(t))^{1/\theta}.$$

The Bernoulli equation and the Verhulst equation ($\theta = 1$), which is a special case of the former, are the simplest way to incorporate density-dependent effects (e.g. competition for the limited resources) into the model. In general, density-dependent population growth models for a single species can be described by a non-linear equation of the form $N'(t) = F(t, N(t)) N(t)$, with a suitable definition of the function F .

Despite of their simplicity, both systems are paradigmatic models from the modelling point of view, although they do not address/consider sexual reproduction explicitly. See for instance the book by J.D. Murray ([61], volume I, chapters 1 and 2) for a nice introduction to basic population models. See also the recent book by H.R. Thieme 2003 [72] which covers (describes/analyzes) a wide range of population dynamics models.

In Thieme's words, it can be said that *biology*, the science of life, has developed its own 'non-mathematical' models, but lately the formulation of the population dynamics in (mathematical) equations, the analysis of these equations, and the reinterpretation of the results in biological terms has become a valuable source of insight.

In a broad sense, a summary of what it has been my/our job as a *biomathematician* during the last few years, can be stated as follows.

Generally, modelling a "real phenomenon" is not an easy task. The starting point is to describe the underlying physical, chemical or biological process in the form of an (infinite dimensional) *dynamical system* in a Banach space, i.e. a system where one state develops into another state over time according to some deterministic law. It is well-known that dynamical systems are

¹Another possible change of variables is $x = N^{-\theta}$, transforming the equation into a linear one.

classified into discrete or continuous, depending on the set of values of the independent variable time: \mathbb{Z} or \mathbb{R} . In the present work we shall consider continuous time and only for non-negative values (*from the present to the future*), giving rise to the so-called irreversible systems. For each time $t \geq 0$, the solution of this type of systems can be seen as an operator in a Banach space such that maps an initial condition to the solution at time t . The latter is the point of view of the theory of semigroups of operators. See e.g. G.F. Webb in [67]. See also [64] and [62].

So, we restrict to both continuous models, and deterministic models (as opposed to stochastic ones) which neglect the influence of random events. However, we allow some kind of randomness or stochasticity in the models, e.g. a random variable can be considered as a model ingredient (see Chapter 2).

If it is not given, an (ad hoc) theorem of existence and uniqueness of solutions must be provided when dealing with infinite-dimensional continuous dynamical systems, e.g. partial differential equations, integral equations, functional equations, delay equations, ... These kind of theorems are usually proved using a fixed point argument (*contraction mapping principle*), see Chapter 2.

After assuring the existence and uniqueness of the solution of the initial value problem, we are faced with the problem of finding *equilibrium states*, i.e. time-independent solutions. These are the simplest solutions and are very important because they constitute the *skeleton* of the dynamics of the system.

If we have succeeded in finding them, we may try to find out their *stability* either local or global. The analysis of the local stability of an equilibrium means to investigate the behaviour of the solutions that are initially close to that equilibrium. The important issue of the stability of equilibria can be sometimes determined using a Liapunov function, but it is generally achieved by both showing that the so-called *growth bound* of an associated semigroup of linear operators is negative, and proving a suitable *principle of linearized stability*. The former is related to the *spectral bound*, i.e. the supremum of the real parts of the spectrum of the infinitesimal generator (see [62] and [74]). The latter means that we must establish a relationship between the stability of the equilibrium states and the stability of the linearized system (see Section 3.4.2 and Appendix A). Actually, in the literature you can find principles of linearized stability for some abstract non-linear evolution equations, specially for the case of semilinear equations. See [68] and [55].

Very often, the spectrum of a linear operator (i.e. the eigenvalues or point spectrum, the continuous spectrum, and the residual spectrum, see e.g. [62]) is *difficult* to compute. However, in the stability analysis of some particular systems, namely, some non-linear evolution equations governed by *accretive operators* in Banach spaces, we can avoid the computation of the spectrum showing the accretiveness of a certain linear operator. We recall that the class of accretive opera-

tors in Banach spaces (see [11]), which arose as an extension of the class of monotone operators in Hilbert spaces, is defined by those operators A such that its resolvent operator $J_\lambda := (I + \lambda A)^{-1}$ is a non-expansive map, i.e. $\|J_\lambda y - J_\lambda \bar{y}\| \leq \|y - \bar{y}\|$. See Appendix A and Section 2.7.

In addition, we can study the ultimate behaviour in time of the solutions, and bifurcations of the parameters of the system as well, i.e. changes in the evolution of the system while varying the values of the parameters. For instance, see Chapter 3 where we have shown the appearance of a limit cycle (isolated periodic orbit) around an equilibrium by means of a Hopf bifurcation. For a Hopf bifurcation theorem in an abstract infinite dimensional setting see [38].

From the modelling point of view, we focus on models of population dynamics coming from the *ecology*. More precisely, the Chapter 2 is devoted to a general model that describes the dynamics of a sequential hermaphrodite species, see Figure 2.1, and the Chapter 3 (see [20]) is devoted to a model for the sexual phase of a particular haplodiploid species (**monogonont rotifers**, see Figure 3.1). Both are (non-linear) continuously age-structured population models taking sexual reproduction into account. Other related fields as epidemiology, medicine, and demography, also lead to mathematically similar population models. For a monograph on the subject of age-structured population dynamics see [31], [53] and [74].

One of the aims of the population dynamics is to study some aspects of the *biological evolution* by means of natural selection.

Darwin's theory of evolution in a nutshell is that organisms produce offspring which vary slightly from their parents, and *natural selection*² will favour the survival of those individuals whose peculiarities render them best adapted to their environment. Darwinian evolution, then, is a two-stage process: random variation as to raw material, and natural selection as the directing force. See [35]. Currently, biological evolution is defined as follows: in the broadest sense, evolution is merely change, and so is all-pervasive: galaxies, populations of live beings, languages, political systems ... all evolve. Specifically, biological evolution is change in the (hereditary) characteristics of populations of organisms that transcend the lifetime of a single individual. The *traits* of the populations that are considered evolutionary are those that are *inheritable* via the *genetic material* from one generation to the next. Biological evolution embraces everything from slight changes in the proportion of different alleles within a population to the successive alterations that led from the earliest protoorganism to snails, bees, giraffes, and dandelions (*taraxacum officinale*).

As some of the parameters appearing in the (ecological) models correspond to inheritable traits of the species under consideration, we can incorporate biological evolution into the models

²The concept of natural selection was developed independently by two scientists, C.R. Darwin (1809-1882) and A.R. Wallace (1823-1913).

defining a sort of dynamics in the parameter space (or a subset of). The latter is called *evolutionary dynamics* or *adaptive dynamics* (see e.g. O. Diekmann in [67]) and it is mostly a sort of sequential substitution of values of the life-history characteristics of the population rather than a strict dynamical system. So, adaptive dynamics is a way of describing how these parameters evolve by the combined action of *random mutation* and *natural selection*. Moreover, assuming the so-called time scales separation, the ecological dynamics (population–short time-scale) and the evolutionary dynamics (trait–long time-scale) can be uncoupled one from each other.

The modern theory of adaptive dynamics stems from *game theory*, see e.g. [16] section 4.9. Originally developed in 1944 by J. von Neumann and O. Morgenstern, see [73], game theory is a mathematical model used to study the outcomes of interactions between *collaborators* and *enemies* in situations in which neither can entirely predict the actions of the other, but can adapt their behaviour according to what they “see” the other doing. J. Maynard-Smith, one of the most renowned and influential evolutionary biologists, applied game theory to interactions between competing individuals of a single species that use different strategies for survival.

In 1982, J. Maynard-Smith published the book entitled “Evolution and the Theory of Games” [58]. In *loc. cit.*, he described the concept of an *evolutionarily stable strategy* (ESS). Roughly speaking, an ESS is a ‘stable collaborative situation’, a strategy that, if adopted by the vast majority of the individuals in a population, will resist invasion by individuals with a new (different) survival strategy. In our analysis, the decisive criterion for the success or failure of an invading/mutant population is its rate of spread in the environmental conditions set by the current established (or resident) population. See for instance the paper [45].

On the other hand, Maynard-Smith was also known for his work on the adaptive value of sexual reproduction and for having demonstrated the twofold cost of sex, also known as the cost of males. This theory suggests that if an asexual individual were introduced into a sexually reproducing population, then asexual reproduction would soon take over. Roughly speaking, his argument can be stated as follows. In a population of sexual individuals, it takes two individuals to produce one. Alone, a female capable of reproducing parthenogenetically can produce as many individuals as any pair of sexually reproducing individuals. Since males contribute nothing to the offspring, the asexual subpopulation will grow twice as fast as its sexual counterpart.

Recently, we and other authors, see e.g. [25], have studied evolutionary dynamics of infinite dimensional parameters, that is, we have considered function-valued evolutionary traits (e.g. the probability distribution function of a transition process between two stages, see Chapter 2). For the computation of evolutionarily stable strategies of infinite dimensional traits/characteristics, we have used the fact that the maximum of a continuous affine/linear functional on a compact

convex set, is attained at an extreme (or extremal) point of the set. So, the problem is infinite dimensional in two senses, namely, state variables belonging to a function space, and function-valued parameters.

Finally, let us remark again that we have considered sexually-reproducing species. The sexual reproduction, typically defined as reproduction involving the fusion of *genomes*, is explicitly considered in all of the investigated models. This feature leads us to analyze from the evolutionary point of view, the proportion between the number of *females* and *males*, the so-called *sex-ratio* of the population. This issue was already addressed by R.A. Fisher in 1930 (see [42], [32] and [31]), predicting an equal sex-ratio (1 : 1) under some simple hypotheses. With regard to the model of sequential hermaphroditism studied in Chapter 2, we have also found a simple situation where the population remains evolutionarily in an equal proportion between females and males, although this does not hold for the general case. The case of age-independent fertility and mortality, where we have shown that individuals change sex when they reach the 69.3% of their life expectancy, is an example of such a situation.

Summarizing, this thesis is about some evolution equations, in infinite dimensional Banach spaces, modelling the dynamics of sexually-reproducing structured populations, with special emphasis on biological evolution driven by natural selection (adaptive dynamics).

1.1 Age-structured populations

The topic of *population dynamics* can be defined as the study of changes in the number and composition of individuals in a population, and the factors that influence those changes. In structured population dynamics, the simplest internal structure is given by the *age* of the individuals since the evolution of age over time proceeds with speed one.

In order to explain what age-structured population dynamics is about, let us start by a warming up exercise: the probably earliest problem of structured populations, namely, the Fibonacci's Rabbits. See e.g. [16] section 1.8.

Leonardo Pisano, also known as Fibonacci, was born in Italy in about 1170 but educated in North Africa, where his father was a diplomat, and died in 1250. His famous book, *Liber abaci*, was published in 1202 and brought decimal or Hindu-Arabic numerals into general use in Europe. In the third section of this book he posed the following question:

A certain man put a pair of rabbits in a place surrounded on all sides by a wall. How many pairs of rabbits can be produced from that pair in a year if it is supposed that

every month each pair begets a new pair which from the second month on becomes productive?

We shall assume that each pair of rabbits is made up by a female and a male. To translate the words into equations, let us define: $u_{j,n}$ to be the number of j -month-old pairs of rabbits (one female and one male) at time n in months; and u_n to be the total number of pairs of rabbits at time n in months. If we decide to census the population just after the births for that month have taken place, then the total population at time n equals to $u_n = \sum_{j=0}^{\infty} u_{j,n}$. Notice that $u_{0,n}$ is the number of newborn pairs of rabbits at time n . If we interpret that the problem assumes implicitly that no rabbits ever die, then the number of j -old pairs at time n equals to the number of $(j+1)$ -old pairs at time $n+1$, for all $j, n \geq 0$. So, we arrive to the following linear difference equation with a ‘boundary condition’ (the number of newborn pairs equals to the number of adult pairs):

$$u_{j+1,n+1} - u_{j,n} = 0, \quad u_{0,n} = \sum_{j=2}^{\infty} u_{j,n}.$$

Using the difference equation above iteratively, the system is transformed into

$$u_{j,n} = \begin{cases} u_{j-n,0} & \text{if } j \geq n \\ u_{0,n-j} = \sum_{i=2}^{\infty} u_{i,n-j} & \text{if } j < n \end{cases}.$$

From the original system we can derive an homogeneous linear recurrence equation for the total number of pairs of rabbits, namely, $u_{n+2} = u_{n+1} + u_n$, for all $n \geq 0$, since

$$\begin{aligned} u_{n+2} &= u_{0,n+2} + \sum_{j=1}^{\infty} u_{j,n+2} = \left(\sum_{j=2}^{\infty} u_{j,n+2} \right) + \left(\sum_{j=1}^{\infty} u_{j-1,n+1} \right) \\ &= \left(\sum_{j=2}^{\infty} u_{j-1,n+1} \right) + u_{n+1} = \left(\sum_{j=2}^{\infty} u_{j-2,n} \right) + u_{n+1} = u_n + u_{n+1}. \end{aligned}$$

Starting by a single newborn pair of rabbits, the answer to the question of the book turns out to be $u_{12} = 233$, that is, the famous Fibonacci sequence:

$$1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, \dots$$

In addition, we can find the asymptotic behaviour of the solutions. Indeed, it is well-known that the solutions of the linear recurrence equation for the total population, are of the form $u_n = c \lambda^n$, $n \geq 0$, where c is an arbitrary constant and λ is given by the so-called characteristic equation $\lambda^2 = \lambda + 1$. So the general solution is $u_n = c_1 \left(\frac{1+\sqrt{5}}{2} \right)^n + c_2 \left(\frac{1-\sqrt{5}}{2} \right)^n$, $n \geq 0$, and the *asymptotic*

growth ratio ($c_1 \neq 0$) turns out to be $\lim_{n \rightarrow \infty} \frac{u_{n+1}}{u_n} = \frac{1+\sqrt{5}}{2} \simeq 1.618 > 1$, the so-called golden ratio.

Now let us consider a problem in continuous time and age which is analogous in some sense to the previous one, namely, a *transport equation* with speed one for $u(a, t)$ the density with respect to age $a \geq 0$ of pairs of rabbits at time $t \geq 0$, i.e. the following linear first-order hyperbolic partial differential equation with a nonlocal boundary condition:

$$\frac{\partial}{\partial t} u(a, t) + \frac{\partial}{\partial a} u(a, t) = 0, \quad u(0, t) = \int_2^\infty u(a, t) da .$$

Integrating along the characteristic curves $a = t + c$, which are straight lines of unit slope, the system is transformed into an integral equation, namely,

$$u(a, t) = \begin{cases} u(a-t, 0) & \text{if } a \geq t \\ u(0, t-a) = \int_2^\infty u(x, t-a) dx & \text{if } a < t \end{cases} .$$

Here, it is also well-known that the asymptotic behaviour of the solutions is given by the so-called persistent solutions, i.e. solutions of the form $u(a, t) = c e^{\lambda(t-a)}$, $a, t \geq 0$, where c is an arbitrary constant and λ is given by the so-called characteristic equation $1 = \int_2^\infty e^{-\lambda x} dx = \frac{e^{-2\lambda}}{\lambda}$, see for instance [74] or [53] for an introduction to the classical linear age-dependent population dynamics.

Finally, calling $P(t) = \int_0^\infty u(a, t) da$ to the total population at time t , one has that the *asymptotic growth ratio* ($c \neq 0$) turns out to be $\lim_{t \rightarrow \infty} \frac{P(t+1)}{P(t)} = e^{\bar{\lambda}} \simeq 1.531 > 1$, where $\bar{\lambda}$ is the unique positive solution of the characteristic equation above. Moreover, in this basic example the system exhibits a type of asymptotic behaviour called balanced or asynchronous exponential growth, i.e. all the solutions $u(a, t)$, $a, t \geq 0$, stabilize in the following sense:

$$\lim_{t \rightarrow \infty} e^{-\bar{\lambda}t} u(a, t) = c e^{-\bar{\lambda}a}, \quad \text{pointwise in } a \geq 0,$$

and

$$\lim_{t \rightarrow \infty} \int_0^\infty |e^{-\bar{\lambda}t} u(a, t) - c e^{-\bar{\lambda}a}| da = 0.$$

Roughly speaking, it could be said that both systems (the discrete one and the continuous one) evolve in a similar way because the former is a discretization of the latter with both time and age step equal to one. In addition, both systems have a strictly dominant eigenvalue which determines the asymptotic behaviour (see e.g. [46]). Finally, notice that the asymptotic growth ratios of both systems are very close (they differ in about 5.4 %).

Summarizing, we have illustrated a simple age-dependent population dynamics problem in discrete and continuous form. In its turn, each version can be formulated in two different ways, with the second way focusing on the *cohorts*, i.e. collections of individuals born at the same time.

Currently the theory of *Structured Population Dynamics* is rather well established, specially age-dependent models and some size-dependent models which can be reduced to the former. There are two families of reducible size-dependent models, namely, those that have a linear individual growth term and those that the individual growth rate is just a function of the total population. For further details see e.g. [60] section I.3.4 and ([49], [27]) respectively.

From the mathematical point of view, there have been mainly two descriptions or approaches to the subject in the form of *Partial Differential Equations* and in the form of *Integral Equations*. The evolution in time of an age-structured population made up of n species or n subclasses of individuals, can be described by

$$\frac{\partial}{\partial t}u(a, t) + \frac{\partial}{\partial a}u(a, t) = \mathbf{G}(u(\cdot, t))(a), \quad u(0, t) = \mathbf{B}(u(\cdot, t)), \quad u(\cdot, 0) = u^0 \quad (1.1)$$

for the (vector) age-density $u(\cdot, t)$ at time $t \geq 0$ in the Banach space $X = L^1(0, \infty; \mathbb{R}^n)$ equipped with the norm $\|\phi\|_{L^1} = \sum_{i=1}^n \int_0^\infty |\phi_i(x)| dx$, where the operator $\mathbf{G} : X \rightarrow X$ is referred as the *aging function*, which can include terms related to mortality, migration, transition, ... , and the mapping $\mathbf{B} : X \rightarrow \mathbb{R}^n$ is the so-called *birth function*, giving the number of newborns per unit of time. Finally, $u^0(a)$, $a \geq 0$, is the known non-negative initial age distribution of the population. On the other hand, the dynamics of an age-structured population can also be described by

$$u(a, t) = \begin{cases} u^0(a - t) + \int_0^t \mathbf{G}(u(\cdot, s))(s + a - t) ds & \text{if } a \geq t \\ \mathbf{B}(u(\cdot, t - a)) + \int_{t-a}^t \mathbf{G}(u(\cdot, s))(s + a - t) ds & \text{if } a < t \end{cases}, \quad (1.2)$$

with the same notation again. The former approach is the smooth version of the problem and the latter comes from the idea of integrating the partial differential equations along the characteristic curves, which is a general method for solving first-order partial differential equations. Under suitable hypotheses, a *mild form* of the partial differential equation (1.1) (i.e. the derivatives exist in some sense) and the integral equation (1.2) are equivalent³, see for instance the book by G.F. Webb [74] or the book by M. Iannelli [53]. In the present work we shall assume that the structuring continuous variables belong to a non-compact real interval, e.g. the positive half-line. We could have considered that individuals of the population have bounded life-span, but it is well-known that this assumption leads to additional problems.

From the biological point of view, we assume that *vital rates* (i.e. fertility and mortality) and transition rates are intrinsic parameters of the model and may depend on the structuring variable and on the population density as well. The latter corresponds with the fact that

³In elementary textbooks of ordinary differential equations you may find a similar situation, namely, in the theorem of Picard the original ordinary differential equation is replaced by an equivalent integral equation.

density-dependence is the general process necessary for the population regulation. In population dynamics, a transition is understood as a change or passage from one stage to another. Examples of transitions are the change from female to male in a sequential hermaphrodite population; the passage from juvenile to adult; the change from virgin to mated, etcetera...

We focus on sexually reproducing populations. So, we assume that there are sex differences among individuals. This point at issue is an important difference with respect to the classical continuous age-structured population models, viz. SHARPE-LOTKA-MCKENDRICK (linear) and GURTIN-MACCAMY (non-linear). The former corresponds with

$$\mathbf{G}(\phi)(a) := -\mu(a)\phi(a), \quad \mathbf{B}(\phi) := \int_0^\infty \beta(x)\phi(x) dx$$

whereas the latter corresponds with

$$\mathbf{G}(\phi)(a) := -\mu(a, \mathcal{P})\phi(a), \quad \mathbf{B}(\phi) := \int_0^\infty \beta(x, \mathcal{P})\phi(x) dx, \quad \text{where } \mathcal{P} := \int_0^\infty \phi(x) dx.$$

These models (see [56] and [48]) do not explicitly take sexual reproduction into account, since both sexes are considered jointly (then the birth rates are averages) or they are models for females with the assumption that males, not considered, are always abundant enough to fertilize all the females. It is worth to mention that the class of population dynamics models with sexual reproduction are inevitably non-linear models because, roughly speaking, the number of births per unit of time must be proportional to the product of the number of females and males present in the population.

We also point out that we are not dealing with pair-formation models. In these type of systems, the state variables are the female population, the male population, and the pairs of individuals, and one has to take into account the process of formation and separation of pairs. See for instance [13] K.P. Hadeler et al. and the references therein.

1.2 Overview

This thesis is divided into two parts.

The first part (Chapter 2) is devoted to a model for the dynamics of a sequential hermaphrodite species, i.e. a population where every individual functions early in life as one sex (specifically as a female) and then switches to the other sex for the rest of its life, and the sex-reversal occurs at a specific age which is considered as a non-negative random variable. This phenomenon happens in a variety of animals including fish species like the sea bream (*sparus aurata*), the anemonefish, the parrotfish and the blue-headed wrasse (*thalassoma bifasciatum*). The evolution in time of the

age-densities of females $f(\cdot, t)$ and males $m(\cdot, t)$ of such a (*protogynous*) population is described by

$$\begin{pmatrix} f(a, t) \\ m(a, t) \end{pmatrix} = \begin{cases} \left[f^0(a-t) \begin{pmatrix} \frac{1-s(a)}{1-s(a-t)} \\ \frac{s(a)-s(a-t)}{1-s(a-t)} \end{pmatrix} + m^0(a-t) \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right] \Pi(a, t, a-t; P) & \text{a.e. } a \geq t \\ \mathcal{B}(f(\cdot, t-a), m(\cdot, t-a)) \begin{pmatrix} 1-s(a) \\ s(a) \end{pmatrix} \Pi(a, t, 0; P) & \text{a.e. } a < t \end{cases},$$

where the superscript 0 refers to the initial condition (at $t = 0$), $s(a)$ is the probability distribution function of the age at sex-reversal, the functional $\mathcal{B}(\phi, \psi)$ is the non-linear (due to the sexual reproduction) birth function giving the influx of newborns, and $\Pi(a, t, c; P) := e^{-\int_c^a \mu(y, P(y+t-a)) dy}$ is the survival probability according to a per capita mortality rate $\mu(a, P(t))$ which depends on the age a , and on the total population $P(t) = \int_0^\infty f(x, t) + m(x, t) dx$, i.e. the integral over the age span of both females and males. In the smooth version of the model, the transition from female to male at age a is given by $\frac{s'(a)}{1-s(a)} f(a, t)$.

In Section 2.2 we give the basic hypotheses of the model and we derive the previous system of non-linear integral equations as well as the smooth version in the form of a nonlocal non-linear first-order hyperbolic partial differential equations (partial integro-differential equations) with boundary (at $a = 0$) and initial (at $t = 0$) conditions. Section 2.3 is devoted to show the existence and uniqueness of global solutions (i.e. they are defined for all time $t \geq 0$) which are non-negative and biologically meaningful for the present model. We introduce additional hypotheses, namely, suitable Lipschitz conditions on the functional $\mathcal{B}(\phi, \psi)$ and on the function $\mu(a, p)$.

In Section 2.4 we show that the system can be reduced to the *intrinsic sex-ratio subspace* $\{(f, m) : sf = (1-s)m\}$, where the dynamics is given by a single non-linear integral equation for the age-density $u(\cdot, t)$ of individuals (of both sexes):

$$u(a, t) = \begin{cases} u^0(a-t) \Pi(a, t, a-t; P) & \text{a.e. } a \geq t \\ \mathcal{B}((1-s)u(\cdot, t-a), su(\cdot, t-a)) \Pi(a, t, 0; P) & \text{a.e. } a < t \end{cases}.$$

In this reduced system, $s(a)$ turns out to be the proportion of males of the population at age a . In Section 2.4.1 an explicit form of the birth function is derived using a Holling type II functional response, i.e.

$$\mathcal{B}(\phi, \psi) := \int_0^\infty \beta(x, \mathcal{P}) \phi(x) dx \frac{\int_0^\infty \gamma(x, \mathcal{P}) \psi(x) dx}{1 + h \int_0^\infty \psi(x) dx}, \quad \text{where } \mathcal{P} := \int_0^\infty \phi(x) + \psi(x) dx,$$

with β being the fertility for females, γ being the “fertility” or efficiency for males, and $h > 0$ is a normalized handling time. The linear chain trick is performed in Section 2.4.2 just to illustrate an example where the model can be reduced to a system of non-linear ordinary differential equations.

Section 2.5 is devoted to the asymptotic behaviour of the solutions as time t tends to infinity. We have determined a sufficient condition for having bounded trajectories and the possibility of non-trivial dynamics. On the other hand we have seen that the *extinction equilibrium* (the trivial solution) is always locally asymptotically stable, displaying the Allee effect, which is a common feature of sexually-reproducing populations.

In Section 2.6 we address the stationary problem, that is, we look for solutions independent of time. We have found that non-trivial steady states are given by the following *decreasing exponential function*

$$u^*(a) = \frac{P^* \Pi_*(a)}{\int_0^\infty \Pi_*(x) dx}, \quad a \geq 0, \quad \Pi_*(a) = e^{-\int_0^a \mu(y, P^*) dy},$$

where $P^* > 0$, the total population at equilibrium, is a solution of the non-linear equation

$$\int_0^\infty (1 + P^* h s(x)) \Pi_*(x) dx = P^* \int_0^\infty \beta(x, P^*) (1 - s(x)) \Pi_*(x) dx \int_0^\infty \gamma(x, P^*) s(x) \Pi_*(x) dx.$$

We end the section by illustrating two cases. The first one is the (non-linear) case of neglecting the competition for the resources, obtaining that there is at most a non-trivial steady state which is unstable. An explicit expression of this equilibrium is given, and the instability is obtained by means of a linearization procedure. The second case, which is rather general, includes some sort of competition and we have found two non-trivial equilibria for each value of the expected age at sex-reversal in a bounded open interval. Both cases are depicted in a bifurcation diagram, for two choices of the parameter $s(a)$. In Section 2.7 we study the local stability of equilibria for the general case. To this end, we rewrite the reduced system as a non-linear evolution equation and then we introduce additional hypotheses, mainly, suitable conditions on the regularity of the functional $\mathbf{B}(\phi) = \mathcal{B}((1 - s)\phi, s\phi)$ and the function $\mu(a, p)$. Thanks to a principle of linearized stability stated in Appendix A, we have determined a sufficient condition for the local stability which is related to the accretiveness of an associated linear operator.

Considering phenotypic evolution in the context of diploid (two series of chromosomes) population models, in Section 2.8 we study the evolutionary dynamics of the age at sex-reversal. The function-valued trait considered is the probability distribution function $s(a)$, $a \geq 0$. Using *diploid inheritance* in a one-locus two-alleles system, the linear system for the invading/mutant *heterozygotes* is derived in Section 2.8.1. Moreover, we have shown that the invading/mutant

homozygotes can be neglected and hence the latter linear system can be simplified. In Section 2.8.2 we have used convex analysis in order to show that an unbeatable strategy or evolutionarily stable strategy (ESS) is a particular Heaviside step function (all individuals of the population change sex at the same age). More precisely, the computation of such an (infinite dimensional) strategy is based on linear/affine optimization on compact convex sets.

Finally, Section 2.9 is devoted to the adaptive value of the sex-ratio of the population at equilibrium of a sequential hermaphrodite species.

The second part (Chapter 3) is devoted to a model for the sexual phase of a particular haplodiploid species (monogonont rotifers) which exhibits the so-called Cyclic Parthenogenesis (both forms of reproduction: non-sexual and sexual). Monogonont rotifers are small micro-invertebrate animals who inhabit aquatic media with seasonal variations. The evolution in time of the age-densities of virgin mictic females $\tilde{v}(\cdot, \tau)$ (male-producing), mated mictic females $m(\cdot, \tau)$ (resting egg-producing), and haploid males $\tilde{h}(\cdot, \tau)$ (only one series of chromosomes) of such a population is described by the following nonlocal non-linear first order hyperbolic partial differential equations

$$\begin{cases} \frac{\partial}{\partial \tau} \tilde{v}(\alpha, \tau) + \frac{\partial}{\partial \alpha} \tilde{v}(\alpha, \tau) + \tilde{\mu} \tilde{v}(\alpha, \tau) &= -\tilde{E} \tilde{H}(\tau) \tilde{v}(\alpha, \tau) \mathcal{X}_{[0, \tilde{T}]}(\alpha) \\ \frac{\partial}{\partial \tau} m(\alpha, \tau) + \frac{\partial}{\partial \alpha} m(\alpha, \tau) + \tilde{\mu} m(\alpha, \tau) &= \tilde{E} \tilde{H}(\tau) \tilde{v}(\alpha, \tau) \mathcal{X}_{[0, \tilde{T}]}(\alpha) \\ \frac{\partial}{\partial \tau} \tilde{h}(\alpha, \tau) + \frac{\partial}{\partial \alpha} \tilde{h}(\alpha, \tau) + \tilde{\delta} \tilde{h}(\alpha, \tau) &= 0 \end{cases}$$

and boundary conditions $\tilde{v}(0, \tau) = B$, $m(0, \tau) = 0$, $\tilde{h}(0, \tau) = b \int_M^\infty \tilde{v}(x, \tau) dx$,

where $\tilde{\mu}$ and $\tilde{\delta}$ are the per capita mortality rates for females and males respectively, \tilde{E} is the male-female encounter rate, B is the recruitment rate of mictic females, b is the fertility of male-producing mictic females, M is the age at maturity for females, and $\tilde{T} \leq M$ is the threshold age of fertilization. The symbol $\mathcal{X}_{[0, \tilde{T}]}(\alpha)$ stands for the characteristic function, namely, its value is 1 if $\alpha \in [0, \tilde{T}]$ and 0 otherwise. The transition from virgin to mated at age α is given by the term $\tilde{E} \tilde{H}(\tau) \tilde{v}(\alpha, \tau) \mathcal{X}_{[0, \tilde{T}]}(\alpha)$, where $\tilde{H}(\tau) = \int_0^\infty \tilde{h}(x, \tau) dx$, i.e. the total population of haploid males at time τ .

Section 3.2 is devoted to the formulation of the model and its assumptions. Since the equation for mated mictic females is uncoupled from the others, we have focused on the equations for the population of virgin mictic females and haploid males. Scaling the units in age, time and population, i.e. $\alpha = M a$, $\tau = M t$, and $\tilde{v}(\alpha, \tau) = B v(a, t)$, $\tilde{h}(\alpha, \tau) = B b M h(a, t)$, we have reduced the number of parameters of the model to only four: the mortality rates $\mu = \tilde{\mu} M$ and $\delta = \tilde{\delta} M$, the threshold age of fertilization $T = \frac{\tilde{T}}{M} \leq 1$, and $E = \tilde{E} B b M^3$ (related to the

male-female encounter rate). Calling $H(t) = \int_0^\infty h(x, t) dx$, the nondimensionalized system is:

$$\begin{cases} \frac{\partial}{\partial t} v(a, t) + \frac{\partial}{\partial a} v(a, t) + \mu v(a, t) &= -E H(t) v(a, t) \mathcal{X}_{[0, T]}(a) \\ \frac{\partial}{\partial t} h(a, t) + \frac{\partial}{\partial a} h(a, t) + \delta h(a, t) &= 0 \end{cases}$$

with boundary conditions $v(0, t) = 1$, $h(0, t) = \int_1^\infty v(x, t) dx$.

In Section 3.3 we address the stationary problem. We have shown that there is only one continuous steady state (this was already done in [19]) which is given by

$$v^*(a) = \begin{cases} e^{-(\mu+EH^*)a} & a \in [0, T] \\ e^{-(\mu a+EH^*T)} & a \in [T, \infty) \end{cases}, \quad h^*(a) = \delta H^* e^{-\delta a},$$

where $H^* > 0$, the total male population at equilibrium, is the unique solution of the transcendental equation $\mu \delta H^* = e^{-(\mu+EH^*T)}$.

In Section 3.4 we study the local stability of the equilibrium solution by means of a linearization procedure. The linear stability analysis reveals that the equilibrium solution is stable for values of the parameters in a large region containing the values used in [19] and [8]. However, a Hopf bifurcation arises for values that perhaps make biological sense. Indeed, in Section 3.5, we have shown that the equilibrium becomes unstable for values of the parameter E larger than the critical value $E_{un}(\mu, \delta, T)$, and a stable limit cycle (isolated periodic orbit) appears.

Section 3.6 is devoted to the computation of the stable periodic orbit. We have designed an explicit numerical scheme based on both analytical and numerical integration along the characteristic curves. Several numerical experiments are presented.

Finally, some remarks on sex-ratio in rotifer populations are given in Section 3.7.

Chapter 2

A model of sequential hermaphroditism

IN THIS CHAPTER we take the integral equations approach because there is a lack of regularity (smoothness) in the system if we consider a general *random variable* as a model ingredient, e.g. if we allow an arbitrary probability distribution function as a model parameter. In addition, we also take a special process of reproduction, the so-called *sex-reversal* or sequential hermaphroditism, letting us to reduce the system to a form similar to standard structured population models.

2.1 Introduction

We are going to introduce a mathematically tractable *continuously structured population model* which takes sexual reproduction into account. Actually this means that there are two structuring variables, let us say for instance, body size or age and gender. It is worth to mention that this family of ecological models are necessarily non-linear and usually rather complex.

In order to fix ideas, let us consider a single sexually-reproducing species living isolated, interacting with the *environment*, competing for limited resources, mating at random, all of its individuals being equal but for their size (any physical measure of the body) and gender: female or male, both diploid (two series of chromosomes). In particular we assume that the population is spatially homogeneous. Here we consider that the environmental conditions related to the competition for resources are defined by the population itself. In the literature, these conditions are generally defined by several weighted population sizes.

For the sake of completeness, we give here a brief description of the several forms of sexual

reproduction, see for instance [32]. Most animal or plant species produce only two types of *gametes* (large/small). In *hermaphrodite populations*¹, a single individual produces both large and small gametes during its lifetime. On the other hand, in *dioecious (or gonochoric) populations*, females and males are separate throughout their lives. Hermaphroditism comes in two forms: *simultaneous* and *sequential*. In the former, an individual produces both kinds of gametes in each breeding season, more or less at the same time. In the latter, an individual functions early in life as one sex and then switches to the other sex for the rest of its life. This second form has, in its turn, two modes, the so-called *protogyny*: female first, and *protandry*: male first.

Among the possibilities stated above, we take the *Sequential Hermaphroditism* (also termed sex-reversal or sex-change) as the form of reproduction of the population. This choice will keep the model at the same degree of complexity as the standard ones, but this time including a form of sexual reproduction explicitly. Moreover, the fact of incorporating a transition between the two sexes, makes the model interesting in order to study the evolution of *sex-ratio* in the population, that is to say, how random mutation and natural selection “act” on the proportion between females and males. More precisely, we will study the sex-ratio indirectly since what we will do is to analyze the evolution of the age at sex-change.

This reproduction system is widespread among fish and invertebrates, and known for a few plants. For instance, about 10 % of fish species are sex changers (9 % protogynous and 1 % protandrous). Some examples cited in the literature are: the blue-headed wrasse² (*thalassoma bifasciatum*), the parrotfish (*scarus* sp.); the clownfish³ or anemonefish (*amphiprion* sp.) and the sea bream⁴ (*sparus aurata*). And just to quote some families of them: serranidae (*epinephelus*), lethrinidae (*lethrinus*), sparidae, gobiidae, pomacanthidae, pomacentridae (*amphiprion*), labridae (*halichoerus*), scaridae (*scarus*, *sparisoma*), synbranchidae and clupeidae.

In sequential hermaphrodite populations, the change from one sex to the other may be induced by environmental or social factors and the transition occurs when individuals attain a specific body size. More precisely, we assume that the size-at-sex-change is genetically determined and may differ for each individual. As a simplifying hypothesis, we are assuming that all the members of the population are born at the same size and the *individual growth rate* (or growth velocity) is just a positive function of size, i.e. $\frac{dx}{dt} = g(x)$ being x and t , size and time respectively. So, all the members attain a specific size at the same age because they spend the same time to reach it.

¹The term hermaphrodite comes from Greek mythology. Hermes was the messenger of the gods, and Aphrodite was the goddess of beauty.

²Labro de cabeza azul in spanish.

³Like the main fish character in the animated movie Finding Nemo!.

⁴Dorada/Orada in spanish/catalan respectively.

Therefore, in this case, sex-reversal occurs at a specific age and it is independent of environmental or social conditions.

Mathematically, the latter assumption is a considerable simplification. It can be shown that there exists a change of variables (see e.g. [60] section I.3.4, or [75] section 5) that transforms the size-dependent problem into an equivalent age-dependent problem. To put it in another way, with the premises above it is not restrictive to consider the sequential hermaphrodite population structured by individuals age instead of by individuals size.

From the biological point of view, we could have considered a density-dependent individual growth rate accounting for environmental or social variations in the transition from one sex to the other, such as the loss of a mate. In a future work we plan to go on in the direction of including such external factors.

From now on and without loss of generality, we deal with a protogynous species, that is to say, we take the transition to be from female to male. The other case, a protandrous population (male first), is absolutely analogous.

Let us consider that the *critical age*, i.e. the age-at-sex-change, is a general non-negative random variable X with *probability distribution function* $s(a)$,

$$P(X \leq a) = s(a), \quad a \geq 0 \text{ age}.$$

In words, the probability that an individual selected at random has critical age less than or equal to age a is given by the function s at a . Hence, $s(a)$ is the probability that an age a arbitrary individual has already changed sex, or equivalently, $1 - s(a)$ is the probability that she has not done it yet. Therefore, the transition occurs according to this cumulative probability. At this point, the probability $s(a)$ is not necessarily the proportion of males at age a in the population, because initially the proportion of males within a range of ages can be arbitrary.

We stress here that the probability distribution function $s(a)$, $a \geq 0$, will be ‘fixed’ or prescribed until it will be considered as a function-valued evolutionary trait (see Section 2.8).

The value of the distribution function at zero, $s(0) \geq 0$, turns out to be the probability of being born as male, or better, the proportion of males at birth. The case that $s(0)$ is different from zero, can be interpreted twofold: some of the individuals switch sex instantaneously when they are born, that is to say, is the limit case of having early critical ages. Or, it could be said that, there are two kinds of males in the population, the so-called *primary males* which are males throughout their lives, and the *secondary males* which have been females when young.

So, the model permits that both sexes may be produced to start with, and the “first sex” (the females) goes on to change later in life. This phenomenon is called *diandry* in the literature and

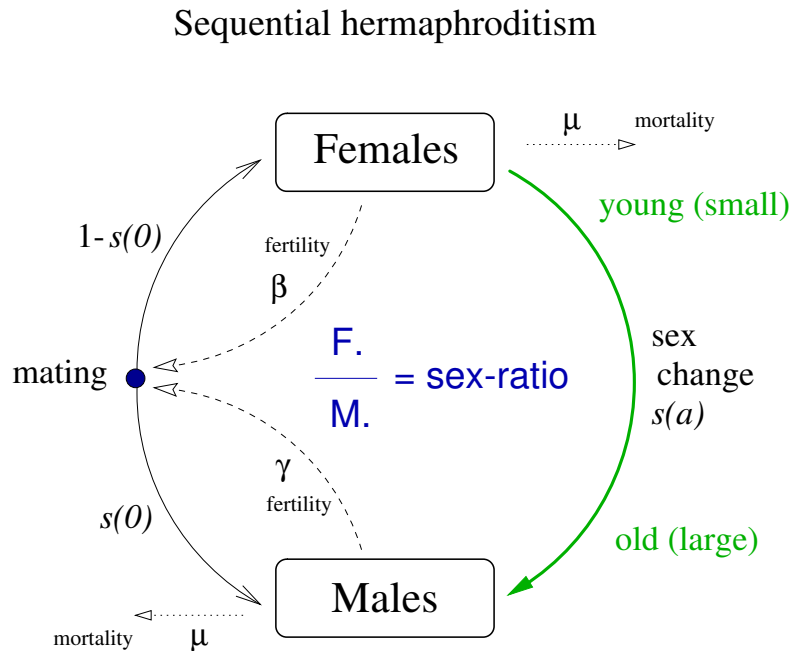


Figure 2.1: Reproductive cycle of a (diandric) protogynous species: female and male offspring are produced in $(1 - s(0)) : s(0)$ proportion, and females change into the other sex later in life at a *critical age* (random variable). Probability of still being female at age a is given by $1 - s(a)$. Vital parameters are: μ mortality, β fertility for females, and γ “fertility” (*efficiency*) for males. Sex-ratio is defined as the proportion between females and males. If $s(0) = 0$ (no diandry) the arrow in the diagram from mating to Males should be removed.

has been observed in parrotfish, for example. On the contrary, the case $s(0) = 0$ simply means that all members are born as females. The diagram in Figure 2.1 shows the reproductive cycle of a protogynous hermaphrodite species, including the possibility of diandry. In this model and on average, females are younger (smaller) than males, i.e. it can be shown that the mean age (mean body-size) of female population at equilibrium is less than or equal to the mean age (mean body-size) of male population at equilibrium. We plan to address this question in a future work.

Finally, the remaining intrinsic parameters: μ the mortality rate for both sexes and β the fertility rate for females (intrinsic vital rates), and γ the “fertility” for males, are age-specific and density dependent. It is natural to assume the same mortality rate for both females and males because they are equal except for their sexual role. The function γ can be interpreted as the *efficiency* or *ability* of males to fertilize eggs, e.g. to compete for females. The dependence of

these parameters on the population size allows us to take into account both *logistic effect* and *Allee effect* (for the latter see [4] and [5]), which affect in an opposite manner the per capita population growth rate. They can be stated as follows. Logistic effect: at high density, an increase of the population size produces a decrease in the per capita fertility rate and an increase in the per capita mortality rate, or equivalently, a decrease in the per capita population growth rate. Allee effect: at low density, an increase of the population size produces an increase in the per capita population growth rate.

2.2 Model formulation

We are going to translate the ecological problem stated in the previous section into mathematical terms. A fairly general (age and sex)-structured population dynamics model of sequential hermaphroditism is formulated. The system takes the form of an *integral equation* issuing from a smooth version of the problem, through the method of integration along characteristic curves. However, we can build the model directly in terms of integral operators instead of differential operators.

So, let us start by introducing the terminology that we are going to use in the sequel.

Let $a, t \in [0, \infty)$ be age and time respectively. Let $X \geq 0$ be the random age when individuals change from female to male (*transition process*) in a sequential hermaphrodite population. From now on we refer to X as the critical age. Let $P(X \leq a) = s(a)$ be the probability distribution function (pdf) of the critical age, so we assume that

Hypothesis 2.1 (random critical age). $s : [0, \infty) \rightarrow [0, 1]$ is non-decreasing, right-continuous and $\lim_{a \rightarrow \infty} s(a) = 1$.

Actually, we should extend s by zero outside of non-negative values, in order to obtain a well-defined pdf on the whole real line. The state variables are: $f(a, t)$ the density with respect to age of female population at time t , and $m(a, t)$ the density with respect to age of male population at time t , which we think as non-negative functions. The total population at time t of each subclass is computed by integrating the corresponding density over the age span. The total population⁵ at time t is simply the sum of both female and male total populations at time t , i.e. $P(t) = \int_0^\infty f(x, t) + m(x, t) dx$.

⁵Notice that the meaning of $P(\cdot)$, the probability of an event or the total population, is determined by the context without confusion.

So, we are in the functional framework of $L^1 := L^1(0, \infty; \mathbb{R})$, the Banach space of equivalence classes of Lebesgue integrable functions from $[0, \infty)$ to \mathbb{R} which agree almost everywhere (a.e.), equipped with the norm $\|\phi\|_{L^1} := \int_0^\infty |\phi(x)| dx$. For the writing simplicity, from now on we shall write $\|\cdot\|_1$ instead of $\|\cdot\|_{L^1}$.

Notice that the state variables are considered as time dependent population densities.

The critical age constrains the state variables in the following sense. The fact that $s(a)$ is the probability, at age a , of having changed from female to male, leads us to the following definition: let a_0 and a_1 be the lower and upper *threshold age* of the transition, that is, the ages when sex-reversal process starts and ends respectively,

$$a_0 := \inf\{a : s(a) > 0\} < \infty, \quad a_1 := \sup\{a : s(a) < 1\}. \quad (2.1)$$

Notice that $0 \leq a_0 \leq a_1$, $s(0)$ and $s(a_0)$ can be both different from zero (and then equal), and $s(a_1) = 1$ due to the right-continuity of function s . We also note that in the previous definition we allow the possibility that the upper threshold age $a_1 = \infty$. Therefore, if a_1 is finite, we can take for almost all ages $a > a_1$, $f(a, t) = 0$. Also, if $a_0 > 0$, we can take for almost all ages $a < a_0$, $m(a, t) = 0$. Indeed, above age a_1 all the (alive) members of the population have changed with probability one, so all of them are almost surely males. Below age a_0 , there is zero probability of changing, so, all individuals are still females with probability one.

Thus, the **sex-ratio** of the population, defined as the proportion between the total female population and the total male population, is computed at time $t \geq 0$ as

$$\frac{\|f(\cdot, t)\|_1}{\|m(\cdot, t)\|_1} = \frac{\int_0^{a_1} f(x, t) dx}{\int_{a_0}^\infty m(x, t) dx}.$$

The birth process of the population is described according to the following general *birth function*. Let $\mathcal{B}(\phi, \psi)$ be the total number of newborn individuals per unit of time, as a function of the age-distribution of their mothers and fathers $\phi, \psi \in L^1$. So we suppose that

Hypothesis 2.2 (birth function). $\mathcal{B} : L^1 \times L^1 \rightarrow \mathbb{R}$ is a non-linear functional such that: $\mathcal{B}(0, \psi) = \mathcal{B}(\phi, 0) = 0$, $|\mathcal{B}(\phi, \psi)| \leq k_1 \|\phi\|_1 \|\psi\|_1$, $|\mathcal{B}(\phi, \psi)| \leq k_2 \|\phi\|_1$ and $\mathcal{B}(L_+^1 \times L_+^1) \geq 0$.

Here, $L_+^1 = \{\phi \in L^1 : \phi(a) \geq 0 \text{ for almost all } a \geq 0\}$ denotes the non-negative cone in the space L^1 . We recall here that L^1 is a Banach lattice such that the norm is additive in the non-negative cone, i.e. $\|\phi + \psi\|_1 = \|\phi\|_1 + \|\psi\|_1$ for all $\phi, \psi \in L_+^1$. The above conditions on the functional \mathcal{B} have the following biological interpretation.

The first condition means that a mother and a father are needed to produce an individual. Second and third assumptions come from the fact that the limiting factor for the number of

newborn individuals, is proportional (k_1) to the number of possible female-male encounters, i.e. total females times total males, and in addition, if we suppose there is some saturation in the input of newborns with respect to male population, then the actual limiting factor is proportional (k_2) to the total females. Finally, the last condition will be needed for the positivity of the solution. More precisely, if the initial condition is non-negative then the solution of the system will remain non-negative for any later time, as we will see in Section 2.3. Positivity has a clear biological meaning, since the number of the individuals cannot be negative. For a given age-distribution of parents at time $t > 0$, let $B(t) := f(0, t) + m(0, t) = (1 - s(0)) \mathcal{B}(f(\cdot, t), m(\cdot, t)) + s(0) \mathcal{B}(f(\cdot, t), m(\cdot, t)) = \mathcal{B}(f(\cdot, t), m(\cdot, t))$ also be the total number of newborn individuals per unit of time, regarded as a function of time, i.e. the total birth rate at time $t > 0$.

Concerning to the mortality process, let $\mu(a, P(t))$ be the age-specific and density dependent per capita mortality rate, so we assume that

Hypothesis 2.3 (mortality rate). $\mu : [0, \infty) \times \mathbb{R} \rightarrow \mathbb{R}$ is positive, locally integrable with respect to age, non-decreasing in population size, and such that:

$$-\mu(a, p) \leq -\inf_{a \geq 0} \mu(a, p) =: -\underline{\mu}(p) \leq -\mu_0 < 0 \text{ a.e. } a \geq 0.$$

Here we point out that if the quantity $\|\mu(\cdot, P(t))(f(\cdot, t) + m(\cdot, t))\|_1$ exists, then it gives the total number of deaths per unit of time, at time t . The dependence of μ on the population size means that there is competition for the limited resources among the members of the population. We remark that the function $\underline{\mu}$, defined in Hypothesis 2.3, is also a non-decreasing function of population size. The constant $\mu_0 > 0$ is interpreted as the minimum mortality, and in particular it is also a lower bound of the mortality in a *virgin environment*, i.e. the mortality when competition effects are not present. From the mortality rate μ we can compute the so-called (density dependent) *survival probability*:

$$\Pi(a, t, c) := e^{-\int_c^a \mu(y, P(y+t-a)) dy} \quad \text{for } c \geq 0, \quad a - c \leq t, \quad (2.2)$$

and if $c \leq a$ it is interpreted as the probability that an individual of age c (at time $t - (a - c)$) will survive to age a at time t when the total population is given by $P(\cdot)$. According to Hypothesis 2.3, the function Π is always positive, decreasing and absolutely continuous in age a , $\Pi(a, t, a) = 1$ for all $a, t \geq 0$, and finally if $c \leq a$ then $\Pi(a, t, c) \leq 1$ and

$$0 \leq \Pi(a, t, c) \leq e^{-\mu_0(a-c)} \xrightarrow{a \rightarrow \infty} 0,$$

excluding the possibility of immortal individuals.

s	the probability distribution function of the random critical age X
\mathcal{B}	the total number of newborns per unit of time (birth function)
μ	the per capita death rate for both females and males

Table 2.1: Function-valued parameters of the model of sequential hermaphroditism.

The parameters of the model, that is to say, the functions appearing in it, are summarized in Table 2.1. For a better understanding of the meaning of the parameters and taking into account that the units of $f(a, t)$, $m(a, t)$ are given in units of population divided by units of time, we recall here the units of the model parameters: $s(a)$ is a dimensionless parameter, $\mathcal{B}(\phi, \psi)$ has units of population \times (time) $^{-1}$, and $\mu(a, p)$ has units of (time) $^{-1}$.

Let $f^0(a)$, $m^0(a)$ be the known female and male initial age distributions constrained by the form of the probability distribution function s , that is, initial conditions that are biologically meaningful for the present model. So we suppose that

Hypothesis 2.4 (initial condition). $f^0, m^0 \in L^1_+$ and the following holds: if $a_1 < \infty$ then $f^0(a) = 0$ for almost all $a > a_1$, and if $a_0 > 0$ then $m^0(a) = 0$ for almost all $a < a_0$.

Taking all the previous Hypotheses (2.1 – 2.4) and definitions into account, in particular the fact that $f(a, t) = 0$ for almost all ages greater than the upper threshold age of the transition process ($a > a_1$) and that $B(t) = \mathcal{B}(f(\cdot, t), m(\cdot, t))$ is the influx of newborns at time t , the model consists of a system of non-linear integral equations⁶:

$$\begin{aligned}
 f(a, t) &= \begin{cases} f^0(a-t) \frac{1-s(a)}{1-s(a-t)} \Pi(a, t, a-t) & \text{a.e. } a_1 > a-t \geq 0 \\ B(t-a) (1-s(a)) \Pi(a, t, 0) & \text{a.e. } a < t \end{cases} & \text{females,} \\
 m(a, t) &= \begin{cases} (f^0 + m^0)(a-t) \Pi(a, t, a-t) - f(a, t) & \text{a.e. } a \geq t \\ B(t-a) s(a) \Pi(a, t, 0) & \text{a.e. } a < t \end{cases} & \text{males,}
 \end{aligned} \tag{2.3}$$

⁶At this point the system is actually a functional equation due to the general form of the birth function \mathcal{B} appearing in the boundary condition. However, we refer to it as an integral equation because the functional \mathcal{B} will be defined in terms of integrals later on, see Section 2.4.1.

with boundary (at $a = 0$) and initial (at $t = 0$) conditions:

$$\begin{aligned} \begin{pmatrix} f(0, t) \\ m(0, t) \end{pmatrix} &= \begin{pmatrix} 1 - s(0) \\ s(0) \end{pmatrix} \mathcal{B}(f(\cdot, t), m(\cdot, t)) \quad t > 0 && \text{birth process,} \\ f(\cdot, 0) = f^0, \quad m(\cdot, 0) = m^0 &&& \text{initial age distributions.} \end{aligned} \quad (2.4)$$

Actually, the boundary and initial conditions are superfluous because they are already given by the integral equations. Nevertheless we have explicitly written them for a better clarity of the exposition. Clearly, the origin $(0, 0)$, the so-called extinction equilibrium, is always a solution of (2.3) since $\mathcal{B}(0, 0) = 0$.

Now we deal directly with the very particular case of upper threshold age $a_1 = 0$, which means that there is no presence of females in the population with probability one, i.e. $\|f(\cdot, t)\|_1 = 0$. This situation happens if and only if the pdf is the characteristic function or *Heaviside step function* $s(a) = \mathcal{X}_{[0, \infty)}(a)$ and it is not interesting from the ecological viewpoint because the population goes exponentially to extinction. Indeed, the influx of newborns is zero in this case, hence $m(a, t) = 0$ for $a < t$ and $m(a, t) = m^0(a - t) \Pi(a, t, a - t)$ for $a \geq t$, and we have that $0 \leq \|m(\cdot, t)\|_1 \leq \|m^0\|_1 e^{-\mu_0 t} \xrightarrow{t \rightarrow \infty} 0$.

So in the following we shall always assume an upper threshold age $a_1 > 0$. In particular $s(0) < 1$.

Clearly, the same asymptotic behaviour occurs if there is no initially female population, that is, if $\|f^0\|_1 = 0$ then the population goes exponentially to extinction. Indeed, taking for granted the existence and uniqueness of global solutions (see Section 2.3), it is a routine to check that $\{(f, m) : f = 0\} \subset L^1 \times L^1$ is a positively-invariant subspace for system (2.3) and on this subspace we have that $\lim_{t \rightarrow \infty} \|m(\cdot, t)\|_1 = 0$, which is derived as before.

With the convention $\frac{f^0(a)}{1-s(a)} := 0$, a.e. $a > a_1 > 0$, let us rewrite system (2.3) for the age-densities of females and males, in a more suitable form:

$$\begin{pmatrix} f(a, t) \\ m(a, t) \end{pmatrix} = \begin{cases} \left[f^0(a-t) \begin{pmatrix} \frac{1-s(a)}{1-s(a-t)} \\ \frac{s(a)-s(a-t)}{1-s(a-t)} \end{pmatrix} + m^0(a-t) \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right] \Pi(a, t, a-t; P) & \text{a.e. } a \geq t \\ \mathcal{B}(f(\cdot, t-a), m(\cdot, t-a)) \begin{pmatrix} 1-s(a) \\ s(a) \end{pmatrix} \Pi(a, t, 0; P) & \text{a.e. } a < t \end{cases} . \quad (2.5)$$

It should be pointed out here that the equations above for females and males are integral equations for the unknown functions f and m in the sense that the function Π , defined in (2.2),

depends on both f and m implicitly through P , the integral over the age span of their sum. The system is somehow similar to the (vector) integral equation studied by G.F. Webb in ([74] p. 21, eq. (1.49)), since if $s(a)$ were sufficiently regular we could write the model in the form of that integral equation.

System (2.3), and hence system (2.5), can be derived as follows.

The evolution in (ecological) time of female and male age-densities is due to both the *transition process* between sexes and the *aging process*. The transition process from female to male, which we have assumed independent of time, is determined by the function $s(a)$, $a \geq 0$, the pdf of the critical age X . Indeed, the probability that a female of age $c < a_1$ has already changed sex at a later age a , i.e. the probability that the transition takes place within the range of ages from c to a is computed as the following conditional probability: $P(X \leq a | X > c) = \frac{P(c < X \leq a)}{P(X > c)} = \frac{s(a) - s(c)}{1 - s(c)}$. Hence, the probability of the complementary event, that is, the probability that a female of age c will remain female at age a is given by $\frac{1 - s(a)}{1 - s(c)}$. On the other hand, the aging process is determined by the density-dependent survival probability Π , as it is usual in age-dependent problems.

So, let us assume firstly that $a_1 > a - t \geq 0$. Then, $f(a - t, 0)$ times the probability of remaining female at age a , times the probability of surviving at age a , gives the density of females at age a and time t , i.e. $f(a, t) = f(a - t, 0) \frac{1 - s(a)}{1 - s(a - t)} \Pi(a, t, a - t)$. On the other hand, the density of males at age a and time $t \leq a$ is given by the sum of two terms: $f(a - t, 0)$ times the probability of not remaining female at age a , times the probability of surviving at age a (that is, alive males that were females at age $a - t$); and $m(a - t, 0)$ times the probability of surviving at age a , i.e.

$$m(a, t) = \left(f(a - t, 0) \frac{s(a) - s(a - t)}{1 - s(a - t)} + m(a - t, 0) \right) \Pi(a, t, a - t).$$

Now let us assume that $a < t$. Then, $f(0, t - a)$ times the probability of remaining female at age a , times the probability of surviving at age a , gives the density of females at age a and time t , i.e. $f(a, t) = f(0, t - a) \frac{1 - s(a)}{1 - s(0)} \Pi(a, t, 0)$, and furthermore $f(0, t - a) = B(t - a) (1 - s(0))$ since the number of newborn females is the number of newborn individuals times the probability of being born as female. On the other hand, the density of males at age a and time $t > a$ is given by the sum of two terms again: $f(0, t - a)$ times the probability of not remaining female at age a , times the probability of surviving at age a (that is, alive males that were born females); and $m(0, t - a)$ times the probability of surviving at age a , i.e.

$$m(a, t) = \left(f(0, t - a) \frac{s(a) - s(0)}{1 - s(0)} + m(0, t - a) \right) \Pi(a, t, 0),$$

and furthermore $m(0, t - a) = B(t - a) s(0)$ because the number of newborn males is the number of newborn individuals times the probability of being born as male. Finally, after some algebra

and realizing that the transition process does not appear when considering females and males jointly, in particular $(f + m)(a - t) = (f^0 + m^0)(a - t) \Pi(a, t, a - t)$ for $a \geq t$, we obtain the integral equations (2.3).

At this moment, this system of equations seems difficult to manage, but it is worth to mention that the dynamics of the system can be readily reduced to a single equation for the density of individuals (of both sexes), as we will see in Section 2.4.

Step functions can be handled rigorously in integral equations. Thus, for instance, system (2.5) includes the case that all individuals change sex at the same age, that is, when the probability distribution function of the critical age is the Heaviside step function $s(a) = \mathcal{X}_{[l, \infty)}(a)$, $l > 0$. We recall that $\mathcal{X}_{[l, \infty)}(a) = 1$ if $a \geq l$, and 0 otherwise. In this situation, all females are exactly younger than males (which have age greater or equal than l), the transition takes place only at age l : $a_0 = a_1 = l$, $s(0) = 0$, and the *expected value of the critical age*, i.e. the expected age at sex-reversal, is $E[X] = l$. This example was studied by E.L. Charnov (see e.g. [32]) but only from the evolutionary point of view.

The smooth version of the present model of sequential hermaphroditism is dealt with until the end of the section.

If we now assume that the critical age X is an absolutely continuous random variable, i.e. its probability distribution function s is an absolutely continuous function, then s is differentiable almost everywhere and can be recovered integrating its derivative s' . In addition, if we also assume that the state variables are sufficiently smooth, then we can rewrite (2.5) as the following system of nonlocal non-linear first-order hyperbolic partial differential equations (partial integro-differential equations) with boundary and initial conditions:

$$\begin{cases} \left. \begin{aligned} f_t(a, t) + f_a(a, t) + \mu(a, P(t)) f(a, t) &= -\frac{s'(a)}{1 - s(a)} f(a, t) \\ m_t(a, t) + m_a(a, t) + \mu(a, P(t)) m(a, t) &= \frac{s'(a)}{1 - s(a)} f(a, t) \end{aligned} \right\} \text{a.e. } a < a_1 \neq 0, \\ \left(\begin{array}{c} f(0, t) \\ m(0, t) \end{array} \right) = \left(\begin{array}{c} 1 - s(0) \\ s(0) \end{array} \right) \mathcal{B}(f(\cdot, t), m(\cdot, t)) \quad t > 0, \\ f(\cdot, 0) = f^0, \quad m(\cdot, 0) = m^0. \end{cases} \quad (2.6)$$

Whereas for almost all $a > a_1$, where a_1 is the upper threshold defined in (2.1), $f(a, t) = 0$ and the second equation above becomes $m_t(a, t) + m_a(a, t) + \mu(a, P(t)) m(a, t) = 0$.

We remark that, the partial differential equations in (2.6) are derived from system (2.5) by computing the ‘directional derivative’ of the population densities, regarded as functions of two

independent variables age and time, in the direction of the vector $(1, 1)$, i.e. $\lim_{h \rightarrow 0} \frac{f(a+h, t+h) - f(a, t)}{h}$ and $\lim_{h \rightarrow 0} \frac{m(a+h, t+h) - m(a, t)}{h}$, with no additional regularity conditions on the parameters \mathcal{B} and μ .

Here the transition process is clearly displayed in the right hand side of the partial differential equations. The term $\frac{s'(a)}{1-s(a)}$ is interpreted as the per capita instantaneous *transition rate* from female to male at age a . Indeed, we can compute the per capita transition rate in an infinitesimal interval of length $da > 0$ as the following limit:

$$\lim_{da \rightarrow 0} \frac{P(X \leq a + da \mid X > a)}{da} = \frac{s'(a)}{1-s(a)} \quad \text{for almost all } a < a_1 \neq 0.$$

So the first equation of (2.6) says that a cohort (collection of individuals born at the same time) in the female subclass decreases by females who get changed and females who die. The second equation says that a cohort in the male subclass increases by those females that become new males and decreases by males who die.

Finally and just to cite another example, let us think about a probability distribution function of the critical age giving a per capita instantaneous transition rate independent of the age of the individuals. The exponential distribution is the only possible one (memoryless critical age), namely, $s(a) = \int_0^a \frac{e^{-x/l}}{l} dx = 1 - e^{-\frac{a}{l}}$, $l > 0$. In this case, s is an absolutely continuous function, the threshold ages of the transition are $a_0 = 0$ and $a_1 = \infty$, i.e. the transition takes place for all ages $a > 0$, and the (constant) per capita transition rate equals to the inverse of the *expected value of the critical age* (the expected value of the feminine period), i.e. $\frac{s'(a)}{1-s(a)} = \frac{1}{E[X]} = \frac{1}{l} > 0$.

Furthermore, the exponential distribution is a particular case of a family of absolutely continuous pdf, namely, the Weibull distribution $s(a) = 1 - e^{-\left(\frac{\Gamma(1+\alpha^{-1})a}{l}\right)^\alpha}$, $E[X] = l > 0$, $\alpha > 0$. In this case, the per capita transition rate turns out to be $\alpha a^{\alpha-1} \left(\frac{\Gamma(1+\alpha^{-1})}{l}\right)^\alpha$, which is a function of age a except for $\alpha = 1$. For large α , this distribution approximates (in the sense that the sequence of random variables converges in law) to the Heaviside step function $H(a - l)$ (the step function considered before), so, the situation where all individuals change sex at approximately the same age, can be modelled by the smooth system (2.6) with this choice of the probability distribution function s .

See for instance the book by H.R. Thieme [72], chapter 12, for an explanation on general stage transitions.

For a monograph on the subject of age-dependent population dynamics see, for instance, the book by G.F. Webb [74] or the book by M. Iannelli [53].

2.3 Existence and uniqueness of solutions

Now we return to the general case, that is to say, the random critical age X is defined by a general probability distribution function and the upper threshold of the transition is positive ($a_1 > 0$). First of all, we need some new definitions and hypotheses (appropriate Lipschitz conditions on \mathcal{B} and μ) in order to prove existence and uniqueness of (local) non-negative solutions to the vector integral equation (2.5) through a fixed point argument in some suitable Banach space. Moreover, at the end of the section we will show that these local solutions are actually ‘globally’ defined, i.e. they are defined for all time $t \geq 0$. The latter is achieved thanks to an a priori bound of the solutions of (2.5).

We remark that all the proofs in this section are based on standard proofs of the theory of age-dependent population dynamics. In order to be precise, all vectors in this section are considered as column vectors and the symbol $|\cdot|$ applied to a vector of any dimension means the sum of the absolute value of its components, as it is usual in population dynamics.

System (2.5) has two components (females and males), so we consider the product space $L^1 \times L^1 \cong L^1(0, \infty; \mathbb{R}^2)$ equipped with the norm $\|(\phi, \psi)\|_1 := \|\phi\|_1 + \|\psi\|_1$, and for $T > 0$ let $L_T := \mathcal{C}([0, T]; L^1 \times L^1)$ be the Banach space of continuous $(L^1 \times L^1)$ -valued functions on the interval $[0, T]$ equipped with the supremum norm $\|(f, m)\|_{L_T} := \sup_{0 \leq t \leq T} \|(f(\cdot, t), m(\cdot, t))\|_1$. The non-negative cone in L_T is denoted by $L_{T,+} := \mathcal{C}([0, T]; L_+^1 \times L_+^1)$.

Let $(f, m) \in L_T$, i.e. the mapping $t \mapsto (f(\cdot, t), m(\cdot, t))$ is continuous from the time interval $[0, T]$ to $L^1 \times L^1$. We say that (f, m) is a *solution* of the integral equation (2.5) on $[0, T]$ provided that $(f(\cdot, t), m(\cdot, t))$ satisfies (2.5) for all $t \in [0, T]$. If, in addition, $(f, m) \in L_{T,+}$ then we say that it is a *non-negative solution*.

Next, two further hypotheses on the birth function and on the mortality rate are introduced. Let $\Phi, \bar{\Phi} \in L^1 \times L^1$, and let $p, \bar{p} \in \mathbb{R}$, so we assume that

Hypothesis 2.5. There exists $c_1(r) > 0$ such that if $\|\Phi\|_1, \|\bar{\Phi}\|_1 \leq r$ then:

$$|\mathcal{B}(\Phi) - \mathcal{B}(\bar{\Phi})| \leq c_1(r) \|\Phi - \bar{\Phi}\|_1.$$

Hypothesis 2.6. There exists $c_2(r) > 0$ such that if $|p|, |\bar{p}| \leq r$ then:

$$|\mu(a, p) - \mu(a, \bar{p})| \leq c_2(r) |p - \bar{p}|.$$

In words, we suppose that the functional \mathcal{B} fulfills a local Lipschitz-continuous condition and that the function μ fulfills a local Lipschitz-continuous condition with respect to population size p and uniformly in age a . In this section and later on we shall write the density-dependent survival

probability as

$$\Pi(a, t, c; P) := e^{-\int_c^a \mu(y, P(y+t-a)) dy} ,$$

thus explicitly showing their dependence on the total population $P(\cdot)$. Next lemma gives a bound of the difference of this probability for two different populations sizes.

Lemma 2.1. *Let Hypotheses 2.3 and 2.6 hold. Let $l, \bar{l} \in L_{T,+}$ such that for all $t \in [0, T]$, $P(t) = \|l(\cdot, t)\|_1 \leq r$ and $\bar{P}(t) = \|\bar{l}(\cdot, t)\|_1 \leq r$, and let $c \geq 0$, $0 \leq a - c \leq t$, then:*

$$|\Pi(a, t, c; P) - \Pi(a, t, c; \bar{P})| \leq c_2(r) |a - c| \|l - \bar{l}\|_{L_T} .$$

Proof. The inequality follows from the fact that $|e^{-x} - e^{-\bar{x}}| \leq |x - \bar{x}|$ for all $x, \bar{x} \geq 0$ (this is a direct consequence of the mean value theorem applied to the negative exponential function) combined with the Lipschitzness of the mortality rate μ , i.e.

$$\begin{aligned} |\Pi(a, t, c; P) - \Pi(a, t, c; \bar{P})| &\leq \left| \int_c^a \mu(y, P(y+t-a)) - \mu(y, \bar{P}(y+t-a)) dy \right| \leq \\ &\leq c_2(r) \int_c^a |P(y+t-a) - \bar{P}(y+t-a)| dy \leq c_2(r) \int_c^a \|l(\cdot, y+t-a) - \bar{l}(\cdot, y+t-a)\|_1 dy \leq \\ &\leq c_2(r) |a - c| \sup_{0 \leq \tau \leq t} \|l(\cdot, \tau) - \bar{l}(\cdot, \tau)\|_1 \leq c_2(r) |a - c| \|l - \bar{l}\|_{L_T} . \end{aligned}$$

□

Now we are ready to state the result which assures the existence and uniqueness of non-negative solutions of the integral equation (2.5) on a time interval $[0, T]$. In addition, the solution will be biologically meaningful in the sense of Hypothesis 2.4, i.e. the solution will represent the population density of a sequential hermaphrodite species (see previous sections for further details). Namely, we have that

Theorem 2.2 (local existence and uniqueness). *Let $r > 0$. Under Hypotheses 2.1–2.6, there exists $T > 0$ such that: if (f^0, m^0) satisfies Hypothesis 2.4 and $\|(f^0, m^0)\|_1 \leq r$, then system (2.5) has a unique solution $(f, m) \in L_{T,+}$. Moreover, for all $t \in [0, T]$ the following holds: if $a_1 < \infty$ then $f(a, t) = 0$ for almost all $a > a_1$, and if $a_0 > 0$ then $m(a, t) = 0$ for almost all $a < a_0$.*

Proof. First of all, we stress that we will use the absolute value even if the functions involved are non-negative, thus showing that the proof without the positivity assumption is very similar.

We will apply the celebrated Banach fixed point theorem, so, for a given initial condition $l^0 = (f^0, m^0) \in L_+^1 \times L_+^1$, $\|l^0\|_1 \leq r$ such that: $f^0(a) = 0$ a.e. $a > a_1$ and $m^0(a) = 0$ a.e. $a < a_0$ according to Hypothesis 2.4, we define the set

$$H = \left\{ l = (f, m) \in L_{T,+} : l(\cdot, 0) = l^0, \|l\|_{L_T} \leq 2r \right\} \subset L_T,$$

which is a closed set in L_T . As before in (2.5), the following convention will make our computation much easier, namely, $\frac{f^0(a)}{1-s(a)} := 0$, a.e. $a > a_1$. Now we define the mapping

$$\mathcal{K} : H \subset L_T \longrightarrow L_T$$

as follows: for $l = (f, m) \in H$, $t \in [0, T]$,

$$\mathcal{K} \begin{pmatrix} f(a, t) \\ m(a, t) \end{pmatrix} = \begin{cases} \left[f^0(a-t) \begin{pmatrix} \frac{1-s(a)}{1-s(a-t)} \\ \frac{s(a)-s(a-t)}{1-s(a-t)} \end{pmatrix} + m^0(a-t) \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right] \Pi(a, t, a-t; P) & \text{a.e. } a \geq t \\ \mathcal{B}(l(\cdot, t-a)) \begin{pmatrix} 1-s(a) \\ s(a) \end{pmatrix} \Pi(a, t, 0; P) & \text{a.e. } a < t \end{cases} \quad (2.7)$$

where $\Pi(a, t, c; P)$ is the survival probability with $P(t) = \int_0^\infty f(x, t) + m(x, t) dx$ being the total population. Notice that the left hand side of (2.7) actually means $(\mathcal{K}l)(a, t)$. We point out here that $\mathcal{K}l$ is defined as the right hand side of the equation (2.5), and that it belongs to L_T . The latter follows from the fact that $\lim_{|t-\bar{t}| \rightarrow 0} \|\mathcal{K}l(\cdot, t) - \mathcal{K}l(\cdot, \bar{t})\|_1 = 0$, which is a consequence of the facts that the functions $t \mapsto \mathcal{B}(l(\cdot, t-a)) \Pi(a, t, 0; P)$ and $t \mapsto \Pi(a, t, a-t; P)$ are continuous from $[0, T]$, and that translation is a continuous operation in L^1 , see [74].

The function \mathcal{K} maps H into itself. Indeed, firstly realize that all three vectors in (2.7) are non-negative and the sum of their components equals to 1. Let $l \in H$, then by the second inequality in Hypothesis 2.2 we have that:

$$\begin{aligned} \|\mathcal{K}l(\cdot, t)\|_1 &\leq \int_0^t |\mathcal{B}(l(\cdot, t-a))| \Pi(a, t, 0; P) da + \int_t^\infty |l^0(a-t)| \Pi(a, t, a-t; P) da \leq \\ &\leq \int_0^t |\mathcal{B}(l(\cdot, t-a))| da + \int_t^\infty |l^0(a-t)| da \leq k_2 \int_0^t \|f(\cdot, t-a)\|_1 da + \int_0^\infty |l^0(a)| da \leq \\ &\leq k_2 t \sup_{0 \leq \tau \leq t} \|f(\cdot, \tau)\|_1 + \|l^0\|_1. \end{aligned}$$

Therefore,

$$\|\mathcal{K}l\|_{L_T} = \sup_{0 \leq t \leq T} \|\mathcal{K}l(\cdot, t)\|_1 \leq k_2 T \|l\|_{L_T} + \|l^0\|_1 \leq (2k_2 T + 1)r \leq 2r, \quad \text{if } T \leq \frac{1}{2k_2}.$$

On the other hand, from (2.7) it readily follows that

$$\mathcal{K}l(\cdot, 0) = f^0(\cdot) \begin{pmatrix} 1 \\ 0 \end{pmatrix} + m^0(\cdot) \begin{pmatrix} 0 \\ 1 \end{pmatrix} = l^0$$

and that $\mathcal{K}l \in L_{T,+}$ since $\mathcal{B}(l(\cdot, t-a)) \geq 0$ for almost all $a < t$, according to the last part of Hypothesis 2.2. Thus proving that $\mathcal{K}(H) \subset H$.

To show that the operator \mathcal{K} is a contraction in the subset H , let $l, \bar{l} \in H$ and for $t \in [0, T]$ set $P(t) = \|l(\cdot, t)\|_1 \leq 2r$ and $\bar{P}(t) = \|\bar{l}(\cdot, t)\|_1 \leq 2r$. Now using the Lipschitzness of \mathcal{B} and Lemma 2.1, the following holds:

$$\begin{aligned} \|\mathcal{K}l(\cdot, t) - \mathcal{K}\bar{l}(\cdot, t)\|_1 &\leq \int_0^t |\mathcal{B}(l(\cdot, t-a)) \Pi(a, t, 0; P) - \mathcal{B}(\bar{l}(\cdot, t-a)) \Pi(a, t, 0; \bar{P})| da + \\ &\quad + \int_t^\infty |l^0(a-t)| |\Pi(a, t, a-t; P) - \Pi(a, t, a-t; \bar{P})| da \leq \\ &\leq \int_0^t |\mathcal{B}(l(\cdot, t-a))| |\Pi(a, t, 0; P) - \Pi(a, t, 0; \bar{P})| + |\mathcal{B}(l(\cdot, t-a)) - \mathcal{B}(\bar{l}(\cdot, t-a))| \Pi(a, t, 0; \bar{P}) da + \\ &\quad + \|l^0\|_1 \sup_{a \geq t} |\Pi(a, t, a-t; P) - \Pi(a, t, a-t; \bar{P})| \leq \\ &\leq k_2 \sup_{0 \leq \tau \leq t} \|f(\cdot, \tau)\|_1 \int_0^t |\Pi(a, t, 0; P) - \Pi(a, t, 0; \bar{P})| da + c_1(2r) \int_0^t \|l(\cdot, t-a) - \bar{l}(\cdot, t-a)\|_1 da + \\ &\quad + \|l^0\|_1 \sup_{a \geq t} |\Pi(a, t, a-t; P) - \Pi(a, t, a-t; \bar{P})| \leq \\ &\leq k_2 \sup_{0 \leq \tau \leq t} \|f(\cdot, \tau)\|_1 c_2(2r) \|l - \bar{l}\|_{L_T} \int_0^t a da + c_1(2r) t \|l - \bar{l}\|_{L_T} + \|l^0\|_1 c_2(2r) t \|l - \bar{l}\|_{L_T}. \end{aligned}$$

Therefore,

$$\begin{aligned} \|\mathcal{K}l - \mathcal{K}\bar{l}\|_{L_T} &\leq \left(k_2 \|l\|_{L_T} c_2(2r) \frac{T^2}{2} + c_1(2r) T + \|l^0\|_1 c_2(2r) T \right) \|l - \bar{l}\|_{L_T} \leq \\ &\leq ((k_2 T + 1) r c_2(2r) + c_1(2r)) T \|l - \bar{l}\|_{L_T}. \end{aligned}$$

Consequently, there exists $T > 0$ small enough such that the mapping \mathcal{K} is a contraction, i.e. $\|\mathcal{K}l - \mathcal{K}\bar{l}\|_{L_T} \leq k \|l - \bar{l}\|_{L_T}$ with $0 \leq k < 1$, and by the contraction principle \mathcal{K} has a unique fixed point $l = (f, m)$ in H . This fixed point is the desired non-negative solution of the integral equation (2.5) on the interval $[0, T]$.

The last part of the theorem follows immediately from the definition of \mathcal{K} in (2.7). \square

We remark that the former theorem as stated is a local existence and uniqueness theorem, in the sense that the interval $[0, T]$ where the solution exists, will depend upon the initial condition, more precisely on its L^1 -norm, that is $T = T(r)$. Global results will follow from this result, by extending solutions to *maximal intervals* of existence, i.e. by using the semigroup (or *semidynamical system*) property.

The remainder of the section is devoted to the problem of continuation of local solutions.

Let $l^0 = (f^0, m^0)$ be a given initial condition. Now, let l be a function from the half-open time interval $[0, T_{\max}(l^0))$ to $L^1 \times L^1$, where $T_{\max}(l^0)$ is the *maximal time* of existence of the solution of (2.5), that is, the maximal time such that if $0 < T < T_{\max}(l^0)$ then there exists the solution of (2.5) on $[0, T]$. We say that l is the (non-negative) solution of (2.5) on $[0, T_{\max}(l^0))$ provided that for all $0 < T < T_{\max}(l^0)$, l restricted to $[0, T]$ is the (non-negative) solution of (2.5) on $[0, T]$.

Next theorem states that if the maximal times of existence were finite, then the solutions would blow up in finite time, i.e. they would become unbounded in finite time.

Theorem 2.3. *Let Hypotheses 2.1–2.6 hold, and let l be the non-negative solution of (2.5) on the time interval $[0, T_{\max}(l^0))$. If $T_{\max}(l^0) < \infty$ then:*

$$\limsup_{t \nearrow T_{\max}(l^0)} \|l(\cdot, t)\|_1 = \infty .$$

Proof. Let us assume that $T_{\max}(l^0) < \infty$ and that there exists $r > 0$ such that $\|l(\cdot, t)\|_1 \leq r$ for $0 \leq t < T_{\max}(l^0)$. Recall that by Theorem 2.2 (local existence and uniqueness), there exists $T = T(r) \in (0, T_{\max}(l^0))$ such that: if $\|\bar{l}^0\|_1 \leq r$ (another initial condition), then system (2.5) with $l^0 = (f^0, m^0)$ replaced by $\bar{l}^0 = (\bar{f}^0, \bar{m}^0)$, has a unique solution on $[0, T]$. Now set $T_1 := T_{\max}(l^0) - \frac{T}{2}$ and let $l = (f, m) \in L_{T_1, +}$ be a solution of (2.5) on $[0, T_1]$ (with initial condition l^0 , of course). Since $\|l(\cdot, T_1)\|_1 \leq r$, there exists $\bar{l} = (\bar{f}, \bar{m}) \in L_T$ such that:

$$\begin{pmatrix} \bar{f}(a, t) \\ \bar{m}(a, t) \end{pmatrix} = \begin{cases} \left[f(a-t, T_1) \begin{pmatrix} \frac{1-s(a)}{1-s(a-t)} \\ \frac{s(a)-s(a-t)}{1-s(a-t)} \end{pmatrix} + m(a-t, T_1) \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right] \Pi(a, t, a-t; \bar{P}) & \text{a.e. } a \geq t \\ \mathcal{B}(\bar{l}(\cdot, t-a)) \begin{pmatrix} 1-s(a) \\ s(a) \end{pmatrix} \Pi(a, t, 0; \bar{P}) & \text{a.e. } a < t \end{cases}$$

with $\bar{P}(t) = \int_0^\infty \bar{f}(x, t) + \bar{m}(x, t) dx$, and $\frac{f(a, T_1)}{1-s(a)} := 0$, a.e. $a > a_1$, that is, a solution of (2.5) on $[0, T]$ but with initial condition $l(\cdot, T_1)$. Finally, setting $T_2 := T_{\max}(l^0) + \frac{T}{2}$, we can extend $l(\cdot, t)$ from $[0, T_1]$ to the interval $[0, T_2]$ by defining $l(\cdot, t) = \bar{l}(\cdot, t - T_1)$ for $t \in [T_1, T_2]$, thus contradicting the definition of $T_{\max}(l^0)$.

Therefore, we must have that $\limsup_{t \nearrow T_{\max}(l^0)} \|l(\cdot, t)\|_1 = \infty$. \square

The last theorem of this section states that the maximal times of existence of solutions of (2.5) are unbounded, and therefore in the forthcoming sections we will be able to study the asymptotic behaviour of solutions as t tends to infinity.

Theorem 2.4 (global existence and uniqueness). *Under Hypotheses 2.1–2.6, the solutions of system (2.5), given by Theorem 2.2, are defined for all $t \geq 0$.*

Proof. Let $l = (f, m)$ be the non-negative solution of (2.5) on $[0, T_{\max}(l^0))$, i.e. the solution given by Theorem 2.2 extended to the interval $[0, T_{\max}(l^0))$ by the semigroup property. Proceeding as in the proof of Theorem 2.2 we have that:

$$\begin{aligned} \|l(\cdot, t)\|_1 &\leq \int_0^t |\mathcal{B}(l(\cdot, t-a))| \Pi(a, t, 0; P) da + \int_t^\infty |l^0(a-t)| \Pi(a, t, a-t; P) da \leq \\ &\leq k_2 \int_0^t \|f(\cdot, \tau)\|_1 d\tau + \int_0^\infty |l^0(a)| da \leq k_2 \int_0^t \|l(\cdot, \tau)\|_1 d\tau + \|l^0\|_1 . \end{aligned}$$

Therefore, by the Gronwall inequality, we obtain the following a priori bound⁷ of the solutions of (2.5):

$$\|l(\cdot, t)\|_1 \leq \|l^0\|_1 e^{k_2 t} \quad 0 \leq t < T_{\max}(l^0) ,$$

and finally, according to Theorem 2.3, we must have $T_{\max}(l^0) = \infty$, i.e. the solutions of (2.5) are defined for all $t \geq 0$. \square

Summarizing, we have seen the existence and uniqueness of global solutions to (2.5), which are non-negative and biologically meaningful for the present model.

In the remainder of the chapter, we will assume the **Hypotheses 2.1–2.6**.

2.4 Reduction to a subspace

One of the methods for simplifying a dynamical system is to reduce the ‘dimensionality’ of the system. For instance, if one can find a submanifold, either finite or infinite dimensional, being an attracting and (positively) invariant subset of the whole state space, then the system can be reduced to that manifold.

The aim of this section is to show that system (2.5) has an infinite dimensional positively invariant *subspace* (or linear manifold) of $L^1 \times L^1$, and that the system reduces to that subspace

⁷We could have obtained a better bound, but it is not necessary for the present proof.

since it is an exponentially attracting subset. In order to do that, we will make a (simple) linear change of variables.

Again, all vectors in this section will be considered as column vectors. If we make an attempt to simplify the system directly by adding both equations in (2.5), we do not obtain a single equation for the density of individuals (of both sexes) because of the birth function. On the other hand, we realize that there is an important relation between female and male densities in (2.5), namely,

$$s(a) f(a, t) = (1 - s(a)) m(a, t), \quad \text{for almost all } a < t.$$

These considerations suggest the following linear change of state variables in (2.5):

$$u(a, t) = f(a, t) + m(a, t), \quad v(a, t) = s(a) f(a, t) + (s(a) - 1) m(a, t).$$

More precisely, for each $t \geq 0$ the change of variables is defined by the following one-to-one bicontinuous (bounded) linear operator $\mathcal{R} : L^1 \times L^1 \longrightarrow L^1 \times L^1$,

$$\mathcal{R} \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ s & s - 1 \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}.$$

Indeed, \mathcal{R} is obviously linear and well-defined in the whole product space since s , the probability distribution function of the critical age, is bounded: $0 \leq s(a) \leq 1$. Moreover \mathcal{R} is a bounded linear operator with norm

$$\|\mathcal{R}\| := \sup_{\|\Phi\|_1=1} \|\mathcal{R}\Phi\|_1 = 2, \quad \text{for } \Phi \in L^1 \times L^1.$$

The latter follows from two facts: for all $\Phi = (\phi, \psi) \in L^1 \times L^1$, we have that $\|\mathcal{R}\Phi\|_1 = \|\phi + \psi\|_1 + \|s\phi + (s - 1)\psi\|_1 \leq 2(\|\phi\|_1 + \|\psi\|_1) = 2\|\Phi\|_1$. And defining $\Phi_n := (\mathcal{X}_{[n, n+1]}, 0) \in L^1 \times L^1$ for $n \geq 0$, we have that $\|\mathcal{R}\| \geq \sup_{n \geq 0} \|\mathcal{R}\Phi_n\|_1 = \sup_{n \geq 0} (1 + \int_n^{n+1} s(x) dx) = 2$.

The inverse of \mathcal{R} can be computed explicitly, which turns out also to be a bounded linear operator on $L^1 \times L^1$ with norm equal to 2, and it is well-defined in the whole space too, namely:

$$\mathcal{R}^{-1} \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} 1 - s & 1 \\ s & -1 \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}, \quad \|\mathcal{R}^{-1}\| = 2.$$

If we set the convention $\frac{v^0(a)}{1-s(a)} := 0$ a.e. $a > a_1$, then the system for the new variables (u, v)

with related initial conditions $(u^0, v^0) := \mathcal{R}(f^0, m^0)$ becomes:

$$\begin{pmatrix} u(a, t) \\ v(a, t) \end{pmatrix} = \begin{cases} \left[u^0(a-t) \begin{pmatrix} 1 \\ 0 \end{pmatrix} + v^0(a-t) \begin{pmatrix} 0 \\ \frac{1-s(a)}{1-s(a-t)} \end{pmatrix} \right] \Pi(a, t, a-t; P) & \text{a.e. } a \geq t \\ \mathcal{B}(\mathcal{R}^{-1}(u(\cdot, t-a), v(\cdot, t-a))) \begin{pmatrix} 1 \\ 0 \end{pmatrix} \Pi(a, t, 0; P) & \text{a.e. } a < t \end{cases} \quad (2.8)$$

where now $P(t) = \int_0^\infty u(x, t) dx$. Since the mapping \mathcal{R} is an isomorphism of Banach spaces, Theorem 2.4 assures the existence and uniqueness of solutions of the integral equation (2.8) for all time $t \geq 0$, although now only the first component of the solution being non-negative. Let us remark that the new state variable u represents clearly the individuals (of both sexes) of the population whereas the new state variable v can be interpreted as a certain ‘measure’ of how far is the actual sex-ratio of the population at age a , which depends on the initial condition, from the sex-ratio determined by the transition process, i.e. $(1-s(a))/s(a)$.

Now it is a routine to check that the vector subspace $\{(u, v) : v = 0\} \subset L^1 \times L^1$ is a positively invariant subspace for system (2.8) and furthermore it is an exponentially attracting set, i.e. we have that:

Proposition 2.5. *Let Hypotheses 2.1–2.6 hold, then:*

(i) *if $v^0 = 0$ then $v(\cdot, t) = 0$ for all $t \geq 0$.*

(ii) *For all $t \geq 0$ $\|v(\cdot, t)\|_1 \leq \|v^0\|_1 e^{-\mu_0 t} \xrightarrow{t \rightarrow \infty} 0$.*

Proof. The first part is trivial. To prove the second part, from (2.8) we realize that $v(a, t) = 0$ for almost all $a < t$. So, if the upper threshold $a_1 < \infty$, then it readily follows that $\|v(\cdot, t)\|_1 = 0$ for all $t > a_1$, whereas if $a_1 = \infty$ then

$$\begin{aligned} 0 \leq \|v(\cdot, t)\|_1 &= \int_t^\infty |v^0(a-t)| \frac{1-s(a)}{1-s(a-t)} \Pi(a, t, a-t; P) da \leq \\ &\leq \int_t^\infty |v^0(a-t)| e^{-\mu_0 t} da = \|v^0\|_1 e^{-\mu_0 t} \xrightarrow{t \rightarrow \infty} 0. \end{aligned}$$

□

And a straightforward consequence of the latter is the following

Corollary 2.6 (intrinsic sex-ratio subspace). *Under Hypotheses 2.1–2.6, the vector subspace*

$$\{(f, m) : s f = (1 - s) m\} \subset L^1 \times L^1$$

is an exponentially attracting positively-invariant subspace for system (2.5).

Therefore, the system of the present model of sequential hermaphroditism (2.5) can be reduced to a single non-linear integral equation for the age-density of individuals (of both sexes), i.e. the following *reduced system*:

$$u(a, t) = \begin{cases} u^0(a - t) \Pi(a, t, a - t; P) & \text{a.e. } a \geq t \\ \mathcal{B}((1 - s) u(\cdot, t - a), s u(\cdot, t - a)) \Pi(a, t, 0; P) & \text{a.e. } a < t \end{cases} \quad (2.9)$$

where we recall that now the total population at time $t \geq 0$ is simply given by $P(t) = \int_0^\infty u(x, t) dx$, and $u^0 \in L^1_+$ is the known (non-negative) initial age distribution of individuals (of both sexes), without any other biological constrain. In this system, the densities of females and males at age a and time $t \geq 0$ are recovered by $\tilde{f}(a, t) = (1 - s(a)) u(a, t)$ and $\tilde{m}(a, t) = s(a) u(a, t)$ respectively, and the sex-ratio of the population at age a is fixed and known a priori since it is independent of time, namely:

$$\text{for all } t \geq 0 : \quad \frac{\tilde{f}(a, t)}{\tilde{m}(a, t)} = \frac{1 - s(a)}{s(a)} \quad \text{a.e. } a > a_0 .$$

Nevertheless, the sex-ratio of the population in (2.9) is still a function of time, that is:

$$\frac{\|\tilde{f}(\cdot, t)\|_1}{\|\tilde{m}(\cdot, t)\|_1} = \frac{\int_0^{a_1} (1 - s(x)) u(x, t) dx}{\int_{a_0}^\infty s(x) u(x, t) dx} .$$

For the sake of completeness, we also recall that the existence and uniqueness of non-negative global solutions of the reduced system is guaranteed, and that the function-valued parameters of the model are: $s(a)$ the pdf of the age of sex-reversal, $\mathcal{B}(\phi, \psi)$ the birth function giving the influx of newborns, and $\mu(a, p)$ the per capita mortality rate ($\Pi(a, t, c; P) = e^{-\int_c^a \mu(y, P(y+t-a)) dy}$ being the survival probability). Let us remark again that in the reduced system, $s(a)$ turns out to be the proportion of males of the population at age a .

From now on, we will focus on the reduced system (2.9), i.e. the original complete system (2.5) reduced to the intrinsic sex-ratio subspace, which represents a significant simplification of the model although the system is still infinite dimensional.

2.4.1 Holling type II: functional response

Until now we have been working with a rather general birth function, see Hypothesis 2.2, which accounts for the number of newborn individuals per unit of time. That is to say, we have not specified any particular form nor expression for the functional \mathcal{B} yet. It is worth to mention that this functional must be necessarily non-linear due to the sexual reproduction, and furthermore, the *feedback* via the environmental conditions that we are going to introduce in this section, exhibits a certain hierarchical structure (see [39]).

Using a time budget argument on female population, we will show that the number of newborns exhibits a *Holling type II functional response* to the male density. Specifically, an explicit form for \mathcal{B} will be derived from a submodel in which female population can be either searching for mates or busy ‘handling the production of new offspring’, e.g. producing eggs. For the classical Holling time budget argument applied to a prey-predator model, see [51] and [52].

So, let $\beta(a, P(t)) \geq 0$ be the age-specific and density-dependent per capita and per male fertility rate for females, measured in units of $(\text{population})^{-1} \times (\text{time})^{-1}$. On the other hand, let $0 \leq \gamma(a, P(t)) \leq 1$ be the age-specific and density-dependent “fertility” for males (dimensionless parameter). For a given total population at time t , the latter is understood as the efficiency or ability of an age a male to fertilize eggs, (see [32] chapter 9).

From now on, the symbol $\langle \cdot, \cdot \rangle$ will denote the *duality pairing* between $L^\infty(0, \infty; \mathbb{R})$ and $L^1(0, \infty; \mathbb{R})$ which is defined as $\langle \varphi, \phi \rangle = \int_0^\infty \varphi(x) \phi(x) dx$. However, when dealing with non-negative functions, we shall write the L^1 -norm instead of the duality pairing, since for any fixed non-negative $\varphi \in L^\infty$, one has that $\langle \varphi, \phi \rangle = \langle \varphi, |\phi| \rangle = \|\varphi \phi\|_1$ for all $\phi \in L^1_+$.

Concerning to the birth process, as well as Hypotheses 2.2 and 2.5 we will assume that:

Hypothesis 2.7 (Holling type II). The birth function $\mathcal{B} : L^1 \times L^1 \rightarrow \mathbb{R}$ is defined as

$$\mathcal{B}(\phi, \psi) := \langle \beta(\cdot, \mathcal{P}), \phi \rangle \frac{\langle \gamma(\cdot, \mathcal{P}), \psi \rangle}{1 + h \langle 1, \psi \rangle}, \quad \text{where } \mathcal{P} := \langle 1, \phi + \psi \rangle,$$

both non-negative functions $\beta(\cdot, p), \gamma(\cdot, p) \in L^\infty(0, \infty; \mathbb{R})$, i.e. they are essentially bounded, and $h > 0$ (normalized *handling* time).

This form of the birth function has a certain asymmetry because we have taken the female perspective. It can be derived as follows.

Let us consider a general sexually-reproducing species (say, a fish species and not necessarily hermaphrodite) mating at random, where the age-densities of females and males are denoted by f and m respectively. Now let us suppose that a large number of *sexual encounters* $n \gg 1$

have taken place for each female of the population in a time interval of length $T > 0$. In order to fix ideas, we can assume that in this interval of time T , large as well, every female arrange (organize) its time successively in looking for mates ($\tau_i > 0$ random searching times) and handling the production of new offspring ($\tilde{h} > 0$ expected handling time), i.e.

$$T = (\tau_1 + \tilde{h}) + (\tau_2 + \tilde{h}) + \cdots + (\tau_n + \tilde{h}) .$$

The expected handling time⁸ does not depend on the number of males (only depends on the species under consideration) whereas the searching time can be considered as a positive random variable τ with expectation proportional to the inverse of the total male population, i.e. $E[\tau] = \frac{k}{\int_0^\infty m(x) dx}$, where the constant $k > 0$ has units of population \times time. So the time T turns out to be also a positive random variable such that, by the law of large numbers,

$$\frac{T}{n} = \tilde{h} + \frac{1}{n} \sum_{i=1}^n \tau_i \simeq \tilde{h} + \frac{k}{\int_0^\infty m(x) dx} .$$

On the other hand, let $\tilde{\beta} \geq 0$ be the per capita and per encounter *female fertility* (e.g. the number of eggs produced by a female per encounter), and let $0 \leq \gamma \leq 1$ be the *male efficiency* (e.g. the fraction of eggs fertilized by a male). Both $\tilde{\beta}$ and γ are considered as age-specific dimensionless parameters. Then, the expected number of newborn individuals of an a -aged female in one encounter equals to $\tilde{\beta}(a) \frac{1}{n} \sum_{i=1}^n \gamma(x_i)$, where x_i $i = 1, \dots, n$ are the ages of the males of the n encounters. Therefore, substituting again arithmetic means by expected values,

$$\left. \begin{array}{l} \text{the expected number of newborns of} \\ \text{an } a\text{-aged female per unit of time} \end{array} \right\} = \frac{\tilde{\beta}(a) \frac{1}{n} \sum_{i=1}^n \gamma(x_i)}{\frac{T}{n}} \simeq \frac{\tilde{\beta}(a) \frac{1}{n} \sum_{i=1}^n \gamma(x_i)}{\frac{k}{\int_0^\infty m(x) dx} + \tilde{h}} \simeq$$

$$\simeq \frac{\tilde{\beta}(a) \frac{\int_0^\infty \gamma(x) m(x) dx}{\int_0^\infty m(x) dx}}{\frac{k}{\int_0^\infty m(x) dx} + \tilde{h}} = \frac{\tilde{\beta}(a) \int_0^\infty \gamma(x) m(x) dx}{k + \tilde{h} \int_0^\infty m(x) dx} .$$

Now, setting $\tilde{h} = k h$ and $\tilde{\beta} = k \beta$ (which is simply a normalization), the expected (total) number of newborns per unit of time is obtained by ‘adding’ the expected number of newborns of each female per unit of time:

$$\int_0^\infty \beta(a) f(a) da \frac{\int_0^\infty \gamma(x) m(x) dx}{1 + h \int_0^\infty m(x) dx} .$$

Notice that the new parameter $h > 0$ has units of (population)⁻¹, whereas $\beta \geq 0$ is measured in units of (population)⁻¹ \times (time)⁻¹, which actually means that the new parameter β is the per

⁸The average time needed by a female before she is able to search for another mate.

capita and per male fertility rate for females. Finally, if we incorporate the effects of crowding and resource limitation in both “fertilities”, i.e. β and γ are density-dependent parameters, then we obtain the explicit form of \mathcal{B} given in Hypothesis 2.7.

Thus, the birth function of the reduced system (2.9) is a non-linear functional on L^1 such that, defining the following three continuous (bounded) linear functionals on L^1 ,

$$\begin{aligned} \mathcal{P} : L^1 &\longrightarrow \mathbb{R}, & \mathcal{P}_2 : L^1 &\longrightarrow \mathbb{R}, & \mathcal{P}_3(p) : L^1 &\longrightarrow \mathbb{R} \\ \phi &\mapsto \int_0^\infty \phi(x) dx & \phi &\mapsto \int_0^\infty s(x) \phi(x) dx & \phi &\mapsto \int_0^\infty \gamma(x, p) s(x) \phi(x) dx \end{aligned} ,$$

and setting $I_1 = \mathcal{P} \phi$, $I_2 = \mathcal{P}_2 \phi$ and $I_3 = \mathcal{P}_3(I_1) \phi$ (as the environmental interaction variables in a broad sense⁹), can be written as:

$$\phi \mapsto \mathcal{B}((1-s)\phi, s\phi) = \int_0^\infty \frac{\beta(x, I_1)(1-s(x))I_3}{1+hI_2} \phi(x) dx .$$

We point out here that this form is an example of what O. Diekmann et al. [39] have called *generalized mass action* since the feedback law exhibits a two-level hierarchical structure.

2.4.2 The linear chain trick

It is well known that there is a special class of continuously age-structured population models which can be written as ordinary differential equations for one or several weighted population sizes. This situation occurs for instance, when vital parameters of the population have special constitutive forms. The reduction (projection), from the infinite dimensional state space to a finite dimensional subspace, is performed by the so-called *linear chain trick* (also affectionately called ‘linear chain trickery’), see for instance [13] and the references therein, [53] chapter V, or [34] section 3.2.

Here we want to illustrate, by means of an example, a case where the mortality is independent of age, both fertilities in Hypothesis 2.7 (Holling type II functional response) are eventually decreasing with respect to age (e.g. a polynomial multiplied by a decreasing exponential), and the critical age is an exponential random variable.

So, we consider the reduced system (2.9), assuming the following particular form for the function-valued parameters μ, β, γ and s : let n_1, n_2 be non-negative integers and let $\alpha_1, \alpha_2 > 0$ be positive constants, then we define $\mu(a, p) := \underline{\mu}(p) \geq \mu_0 > 0$ (i.e. do not depend on age a),

$$\begin{aligned} \beta(a, p) &:= \beta_0(p) + \sum_{n=0}^{n_1} \beta_{n+1}(p) a^n e^{-\alpha_1 a} \geq 0 , \\ 0 \leq \gamma(a, p) &:= \gamma_0(p) + \sum_{n=0}^{n_2} \gamma_{n+1}(p) a^n e^{-\alpha_2 a} \leq 1 , \end{aligned}$$

⁹In this model, there are two types of interactions, namely, the interactions due to the competition for the resources and the interactions due to the sexual reproduction.

and $s(a) := 1 - e^{-\frac{a}{l}}$, $l > 0$ (i.e. the critical age is exponentially distributed with expected value l). Then we introduce the compound variables or “*moments*”, i.e the following weighted population sizes:

$$\begin{cases} F(t) = \int_0^\infty (1 - s(x)) u(x, t) dx, & F_n(t) = \int_0^\infty x^n e^{-\alpha_1 x} (1 - s(x)) u(x, t) dx & n = 0, \dots, n_1 \\ M(t) = \int_0^\infty s(x) u(x, t) dx & M_n(t) = \int_0^\infty x^n e^{-\alpha_2 x} s(x) u(x, t) dx & n = 0, \dots, n_2 \end{cases}, \quad (2.10)$$

as a new state variables (sufficiently regulars). Here $P(t)$, the total population at time t , is given by $F + M$, whereas the birth rate at time t , $B(t) = \mathcal{B}((1 - s)u(\cdot, t), s u(\cdot, t))$, turns out to be

$$B(t) = \left(\beta_0(P) F + \sum_{n=0}^{n_1} \beta_{n+1}(P) F_n \right) \left(\gamma_0(P) M + \sum_{n=0}^{n_2} \gamma_{n+1}(P) M_n \right) \frac{1}{1 + h M}.$$

Now, differentiating in (2.10) with respect to time and using the nonlocal non-linear first-order hyperbolic partial differential equation $u_t + u_a + \underline{\mu}(P) u = 0$, with boundary condition $u(0, t) = \mathcal{B}((1 - s)u(\cdot, t), s u(\cdot, t))$, which is obtained from (2.9) by computing the (1, 1)-directional derivative of $u(a, t)$, we get the following non-linear (autonomous) system of ordinary differential equations:

$$\begin{cases} \dot{F} = & B & - \underline{\mu}(P) F - \frac{F}{l} \\ \dot{M} = & & - \underline{\mu}(P) M + \frac{F}{l} \\ \dot{F}_0 = & B & - (\alpha_1 + \underline{\mu}(P)) F_0 - \frac{F_0}{l} \\ \dot{M}_0 = & & - (\alpha_2 + \underline{\mu}(P)) M_0 + \frac{F_0}{l} \\ \dot{F}_n = & n F_{n-1} & - (\alpha_1 + \underline{\mu}(P)) F_n - \frac{F_n}{l} & n = 1, \dots, n_1 \\ \dot{M}_n = & n M_{n-1} & - (\alpha_2 + \underline{\mu}(P)) M_n + \frac{F_n}{l} & n = 1, \dots, n_2 \end{cases},$$

with an initial condition ($t = 0$) related to the initial age distribution $u^0 \in L_+^1$. Notice that this *projected system* has dimension $(4 + n_1 + n_2)$ and preserves positivity. Once we know the non-negative solution of this system at time $t \geq 0$, $P(t)$ and $B(t)$ are known, and the density of individuals $u(\cdot, t)$ at time t is recovered by (2.9).

Finally a particular case of the latter system happens when fertilities are also age independent, i.e. $\beta(a, p) := \beta_0(p)$ and $\gamma(a, p) := \gamma_0(p)$, namely:

$$\begin{cases} \dot{F} = & \left(\frac{\beta_0(P) \gamma_0(P) M}{1 + h M} - \underline{\mu}(P) - \frac{1}{l} \right) F \\ \dot{M} = & - \underline{\mu}(P) M + \frac{F}{l} \end{cases}$$

which is a two-dimensional system for the total female and male populations ($F + M = P$), where one can take advantage of the phase-plane analysis. For instance, one can apply the Poincaré-Bendixson theory and the Dulac criterion.

See [72] chapter 11, for a general one-species two-stage structured population model, which however, does not explicitly take sexual reproduction into account.

2.5 Asymptotic behaviour

Now we come back to the infinite dimensional system (2.9) with s, \mathcal{B}, μ being arbitrary parameters according to Hypotheses 2.1 – 2.7. We recall that the solutions of this reduced system $u(\cdot, t) \in L_+^1$ are defined for all non-negative time and cannot be unbounded in finite time, i.e.

$$0 \leq P(t) \leq P(0) e^{k_2 t}, \quad t \geq 0.$$

It is a common belief in ecology that no given population can grow beyond a certain limit.

Keeping the latter in mind, the aim of this section is to find a suitable sufficient condition which assures that $\limsup_{t \rightarrow \infty} P(t) < \infty$ (the system is *dissipative*), i.e. to see that the solutions of the system remain bounded for all $t \geq 0$. See for instance [74] chapter 4. Moreover, we will obtain that the *extinction equilibrium* is always locally asymptotically stable: if $P(0)$ is small enough then $\lim_{t \rightarrow \infty} P(t) = 0$, displaying the so-called Allee effect.

The asymptotic behaviour of the solutions as t tends to infinity can be determined thanks to the fact that system (2.9) is equivalent to a mild form of a partial differential equation (see [74]) which in particular implies the following inequality:

$$\dot{P}(t) := \limsup_{h \searrow 0} \frac{P(t+h) - P(t)}{h} \leq B(t) - \int_0^\infty \mu(x, P(t)) u(x, t) dx, \quad t \geq 0. \quad (2.11)$$

Throughout this section, the symbol ‘dot’ is understood in the sense of the previous definition.

On the other hand, the influx of the newborns $B(t) = \mathcal{B}((1-s)u(\cdot, t), s u(\cdot, t))$ is such that $B(t) \leq k_1 (P(t))^2$ and $B(t) \leq k_2 P(t)$, $t \geq 0$ (see Hyp. 2.2), and without loss of generality the minimum mortality can be taken such that $\mu_0 = \underline{\mu}(0) \leq \underline{\mu}(P(t))$, $t \geq 0$.

Next proposition states the boundedness of the trajectories of (2.9), namely

Proposition 2.7. *Let Hypotheses 2.1 – 2.7 hold. Assume that there exists*

$$K > 0 \text{ such that } \mathcal{B}((1-s)\phi, s\phi) - \int_0^\infty \mu(x, \|\phi\|_1) \phi(x) dx \leq 0 \text{ for all } \phi \in L_+^1, \|\phi\|_1 \geq K. \quad (2.12)$$

Then:

$$P(t) = \|u(\cdot, t)\|_1 \leq \max\{K, \|u^0\|_1\} < \infty \text{ for all } u^0 \in L_+^1 \text{ and } t \geq 0.$$

Proof. Combining (2.11) and (2.12) we have that there exists $K > 0$ such that

$$\dot{P}(t) \leq \mathcal{B}((1-s)u(\cdot, t), s u(\cdot, t)) - \int_0^\infty \mu(x, \|u(\cdot, t)\|_1) u(x, t) dx \leq 0$$

whenever $P(t) = \|u(\cdot, t)\|_1 \geq K$. Hence, we must have that if $P(0) = \|u^0\|_1 > K$ then $P(t) \leq P(0)$ for all $t \geq 0$.

On the other hand, to prove that if $P(0) \leq K$ then $P(t) \leq K$ for all $t \geq 0$, let us assume the contrary: $P(0) \leq K$ and there exists a time $t_1 > 0$ such that $P(t_1) > K$. By the continuity of $P(t)$ on $[0, t_1]$, there exists $h > 0$ such that $P(0) \leq K < P(t_1 - h) < P(t_1)$. But, using the inequality above we have that $\dot{P}(t) \leq 0$ for all $t \in [t_1 - h, t_1]$, which is a contradiction.

Thus proving the statement. \square

A straightforward consequence of the latter is that the closed ball $\{\phi \in L_+^1 : \|\phi\|_1 \leq K\}$ is a positively-invariant set for system (2.9). Actually, if we change the symbol ' \leq ' by ' $<$ ' in (2.12) then in addition this ball is an attracting set, because $\dot{P}(t)$ is less or equal than a quantity which is negative outside the ball.

Condition (2.12) can be expressed in words as follows: at high population density, the number of individuals who die exceeds the number of newborn individuals. This is a reasonable condition which is often required in population dynamics.

A sufficient condition, for instance, to assure (2.12) is: $\mu_0 < k_2 < \lim_{p \rightarrow \infty} \underline{\mu}(p)$. Indeed, in this case there exists $K = \underline{\mu}^{-1}(k_2) := \inf\{p \geq 0 : k_2 < \underline{\mu}(p)\} > 0$, recall that $\underline{\mu}$ is non-decreasing and therefore we can introduce its *generalized inverse function*, and we have that $\mathcal{B}((1-s)\phi, s\phi) - \int_0^\infty \mu(x, \|\phi\|_1) \phi(x) dx \leq (k_2 - \underline{\mu}(\|\phi\|_1)) \|\phi\|_1 < 0$ for all $\phi \in L_+^1, \|\phi\|_1 > K$.

2.5.1 Stability of the trivial solution

The behaviour of the solutions in the vicinity of the origin (the trivial equilibrium, also called extinction equilibrium) can be determined, without using any linearization procedure, by means of a *Liapunov function*. In continuously structured population models it is usual to take the L^1 norm as a Liapunov functional.

So, next proposition states the stability of the zero solution of the reduced system (2.9), or equivalently, the possibility that the population becomes extinct as t tends to infinity.

Proposition 2.8. *Let Hypotheses 2.1 – 2.7 hold.*

(i) *If $P(0) < \frac{\mu_0}{k_1}$ then $P(0) \geq P(t) \xrightarrow{t \rightarrow \infty} 0$, i.e.*

the trivial equilibrium of (2.9) is locally asymptotically stable.

(ii) If $k_2 < \mu_0$ then the population goes to extinction, i.e.

the trivial equilibrium of (2.9) is globally asymptotically stable.

Proof. Using (2.11) again we have that: $\dot{P}(t) \leq (k_1 P(t) - \mu_0) P(t) < 0$ whenever $0 < P(t) < \frac{\mu_0}{k_1}$, and if $k_2 < \mu_0$ then $\dot{P}(t) \leq (k_2 - \mu_0) P(t) < 0$ whenever $0 < P(t)$. So, by the Liapunov direct method, the statement follows. \square

Before closing this section, let us make a few comments. The fact that the trivial equilibrium is always locally asymptotically stable, the result (i) above, agrees with the idea that for some species that reproduce sexually, an initially low population density produces the extinction of the population. On the other hand, the result (ii) above is a classical statement in population dynamics which means that if the *minimum mortality* exceeds the *maximum fertility* then there is no possibility of non-trivial dynamics.

From now on, for the general case where we consider competition for the resources, we shall assume that $\mu_0 < k_2$ and that condition (2.12) holds with strict inequality for a positive constant K such that $\frac{\mu_0}{k_1} < K$, thus having bounded trajectories and the possibility of non-trivial dynamics, see Propositions 2.7 and 2.8.

2.6 Non-trivial steady states

We look for steady states (equilibria) of the reduced system (2.9), i.e solutions independent of time. Since the extinction equilibrium has been already analyzed, now we are interested in non-trivial steady states $u^* \in L_+^1$.

This kind of solutions are obtained as follows. First of all, let us call $P^* = \|u^*\|_1$ the total population at equilibrium and $\Pi_*(a) := e^{-\int_0^a \mu(y, P^*) dy}$, $a \geq 0$, the (density dependent) survival probability at equilibrium. The latter is interpreted as the probability at birth of living to age a when the population is at equilibrium, that is, $0 < \Pi_*(a) = \Pi(a, \cdot, 0; P^*) \leq 1$. It follows from system (2.9) that stationary solutions of the form $u(a, t) = u^*(a)$ must satisfy the relation

$$u^*(a) = \begin{cases} u^*(a-t) \frac{\Pi_*(a)}{\Pi_*(a-t)} & \text{a.e. } a \geq t \\ \mathcal{B}((1-s)u^*, su^*) \Pi_*(a) & \text{a.e. } a \geq 0 \end{cases}.$$

First relation implies that $\frac{u^*(a)}{\Pi_*(a)} = \frac{u^*(a-t)}{\Pi_*(a-t)}$, $a \geq t$, hence $u^*(a) = u^*(0) \Pi_*(a)$, $a \geq 0$, since $\Pi_*(0) = 1$, and the latter implies that $P^* = u^*(0) \|\Pi_*\|_1$, which is obtained integrating over the

age span. Thus, isolating $u^*(0)$ we get

$$u^*(a) = \frac{P^*}{\|\Pi_*\|_1} \Pi_*(a), \quad a \geq 0, \quad (2.13)$$

or in the standard notation (recall that $\|\cdot\|_1$ means the L^1 -norm):

$$u^*(a) = \frac{P^* e^{-\int_0^a \mu(y, P^*) dy}}{\int_0^\infty e^{-\int_0^x \mu(y, P^*) dy} dx}, \quad a \geq 0.$$

Finally, the second relation above combined with the formula (2.13) imply that the total population at equilibrium P^* , regarded as a non-negative independent variable, solves the scalar non-linear equation:

$$Q = \mathcal{B}((1-s)Q\Pi_*, sQ\Pi_*), \quad \text{with } Q = \frac{P^*}{\|\Pi_*\|_1}. \quad (2.14)$$

Therefore, for each positive solution $P^* > 0$ of (2.14) there exists a non-trivial steady state $u^* \in L^1_+$ of (2.9) given by the formula (2.13). Furthermore, u^* turns out to be a (non-constant) absolutely continuous function, and recalling that the birth function takes the form of a *Holling type II functional response*, i.e. $\mathcal{B}((1-s)Q\Pi_*, sQ\Pi_*) = \|\beta(\cdot, P^*) (1-s)Q\Pi_*\|_1 \frac{\|\gamma(\cdot, P^*)sQ\Pi_*\|_1}{1+h\|sQ\Pi_*\|_1}$, equation (2.14) can be written for $P^* > 0$ as

$$\|(1 + P^* h s)\Pi_*\|_1 = P^* \|\beta(\cdot, P^*) (1-s)\Pi_*\|_1 \|\gamma(\cdot, P^*) s\Pi_*\|_1, \quad (2.15)$$

or in the standard notation:

$$\int_0^\infty (1 + P^* h s(x)) \Pi_*(x) dx = P^* \int_0^\infty \beta(x, P^*) (1-s(x)) \Pi_*(x) dx \int_0^\infty \gamma(x, P^*) s(x) \Pi_*(x) dx.$$

Concerning with this scalar non-linear equation, multiple situations can occur depending on the vital parameters of the population, as it is usual in the steady state analysis of age-dependent population dynamics. However, we can undertake a qualitative study of equation (2.14) or (2.15) according to some parameter, for instance the probability distribution function s , and keeping the others fixed (β, γ, h and μ).

Here we want to discuss briefly necessary conditions for the existence of non-trivial steady states versus the *projected 'parameter'* $E[X] = \int_0^\infty (1-s(x)) dx > 0$, the expected critical age. The latter formula is obtained integrating by parts, see e.g. [72] section 12.9. To this end, let us take into account the assumptions on the birth function \mathcal{B} given in Hypothesis 2.2, and the results about the asymptotic behaviour of the solutions given in Section 2.5. Therefore, if P^* is a positive solution of (2.14) then the following inequalities hold:

$$E[X] \geq \frac{1}{k_2}, \quad \frac{\mu_0}{k_1} \leq P^* \leq K, \quad \text{and} \quad P^* \geq \frac{1}{k_1 E[X]}. \quad (2.16)$$

Indeed, the first inequality is a direct consequence of $0 < Q = \mathcal{B}((1-s)Q\Pi_*, sQ\Pi_*) \leq k_2 \|1-s\|_1 Q \|\Pi_*\|_\infty \leq k_2 E[X]Q$, where $\|\cdot\|_\infty$ stands for the L^∞ -norm. Similarly, the second one follows from $0 < Q = \mathcal{B}((1-s)Q\Pi_*, sQ\Pi_*) \leq k_1 \|1-s\|_\infty Q \|\Pi_*\|_1 \|s\|_\infty Q \|\Pi_*\|_1 \leq k_1 Q P^* \|e^{-\mu_0 \cdot}\|_1$. The third one above, $P^* \leq K$, deserves a special attention. Indeed, let us assume that the solution of equation (2.14) is such that $P^* > K$, and that condition (2.12) holds with strict inequality, then $0 < Q = \mathcal{B}((1-s)Q\Pi_*, sQ\Pi_*) < \int_0^\infty \mu(x, P^*) Q \Pi_*(x) dx = Q$ which is a contradiction. Finally, the last inequality in (2.16) is derived in a similar way $0 < Q = \mathcal{B}((1-s)Q\Pi_*, sQ\Pi_*) \leq k_1 \|1-s\|_1 Q \|\Pi_*\|_\infty \|s\|_\infty Q \|\Pi_*\|_1 = k_1 E[X]Q P^*$.

The inequalities in (2.16) define a kind of *horizontally unbounded strip* (a vertically bounded region) strictly contained in the positive quadrant of the $(E[X], P^*)$ -plane, see Figures 2.2 and 2.3 (bifurcation diagrams). Outside this region, there is no non-trivial equilibrium. In particular, populations with an early expected critical age, cannot attain any non-trivial equilibrium.

Let us remark that the sex-ratio of the population at equilibrium is $\frac{\|(1-s)\Pi_*\|_1}{\|s\Pi_*\|_1} \leq \frac{E[X]}{\|s\Pi_*\|_1}$.

2.6.1 An explicit case: neglecting competition

In this section we are going to analyze the dynamics of the present model of sex-reversal assuming that the resources are unlimited. So, the effect of competition for the resources is neglected and we can take the its related environmental conditions to be constant (i.e. independent of the population size). However, the interactions due to the sexual reproduction are still present.

More precisely, without loss of generality, the vital parameters of the population in a virgin environment can be taken as:

$$\beta_0(a) := \beta(a, 0) \geq 0, \quad 0 \leq \gamma_0(a) := \gamma(a, 0) \leq 1, \quad \mathcal{B}_0(\phi, \psi) := \langle \beta_0, \phi \rangle \frac{\langle \gamma_0, \psi \rangle}{1 + h \langle 1, \psi \rangle},$$

$$\text{and } 0 < \Pi_0(a) := e^{-\int_0^a \mu(y, 0) dy} \leq 1.$$

Here we assume that the birth function \mathcal{B}_0 , which is a non-linear functional on $L^1 \times L^1$ but however is linear in the first variable, fulfills an assumption like Hypothesis 2.2. On the other hand, we also assume that the inequality giving the possibility of non-trivial dynamics $\mu_0 < k_2$ holds, and the condition assuring bounded trajectories (2.12) is disregarded. Therefore, the system neglecting the effect of competition, which is still non-linear due to the sexual reproduction, is:

$$u(a, t) = \begin{cases} u^0(a-t) \frac{\Pi_0(a)}{\Pi_0(a-t)} & \text{a.e. } a \geq t \\ \mathcal{B}_0((1-s)u(\cdot, t-a), s u(\cdot, t-a)) \Pi_0(a) & \text{a.e. } a < t \end{cases}. \quad (2.17)$$

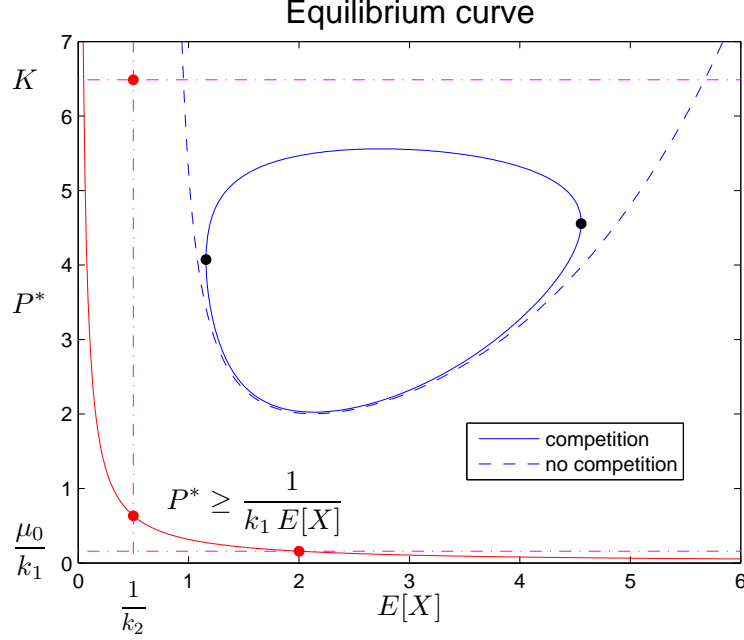


Figure 2.2: The case of a step function $s(a) = \mathcal{X}_{[l, \infty)}(a)$, $E[X] = l > 0$, i.e. sex-reversal takes place only at age l . The picture shows the total population at equilibrium (*solid line*) of the reduced system (2.9) varying the *projected ‘parameter’* $E[X]$, i.e. the closed continuous curve (l, P^*) implicitly defined by equation (2.15), which is confined inside the horizontally unbounded strip defined by (2.16). Neglecting the effect of competition, the equilibrium curve becomes the graph of an unbounded function (*dashed line*). See Sections 2.6.1 and 2.6.2 for further details.

Notice that here we also use the name $u(a, t)$ for the population density, and that (2.17) is actually a formula for ages $a \geq t$.

Most of the features of system (2.9) are *inherited* by system (2.17), namely, the zero solution is also always locally asymptotically stable, and the non-trivial equilibria are also given by a decreasing exponential function $u^*(a) = \frac{P^*}{\|\Pi_0\|_1} \Pi_0(a)$, $a \geq 0$, although now the equation for $P^* > 0$: $1 = \mathcal{B}_0((1-s)\Pi_0, s \frac{P^*}{\|\Pi_0\|_1} \Pi_0)$, or equivalently $\|(1 + P^* h s)\Pi_0\|_1 = P^* \|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s \Pi_0\|_1$ turns out to be linear. Consequently, the total population at equilibrium $P^* > 0$ is explicitly given by

$$P^* = \|\Pi_0\|_1 \left(\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s \Pi_0\|_1 - h \|s \Pi_0\|_1 \right)^{-1},$$

whenever the parenthesis above is positive.

Summarizing, for any set of values of the parameters $s(\cdot), \beta_0(\cdot), \gamma_0(\cdot), h$ and $\mu(\cdot, 0)$ such that

$(\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s\Pi_0\|_1 - h\|s\Pi_0\|_1) > 0$, there exists a unique non-trivial stationary solution $u^* \in L^1_+$ of the no-competition system (2.17), explicitly given by

$$u^*(a) = (\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s\Pi_0\|_1 - h\|s\Pi_0\|_1)^{-1} \Pi_0(a), \quad a \geq 0, \quad (2.18)$$

or in the standard notation:

$$u^*(a) = \left(\int_0^\infty \beta_0(x)(1-s(x))\Pi_0(x) dx \int_0^\infty \gamma_0(x)s(x)\Pi_0(x) dx - h \int_0^\infty s(x)\Pi_0(x) dx \right)^{-1} \Pi_0(a).$$

On the contrary, for values such that $(\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s\Pi_0\|_1 - h\|s\Pi_0\|_1) \leq 0$, there is no non-trivial stationary solution to system (2.17). See Figures 2.2 and 2.3 for a plot (dashed line) of the total population of the equilibrium solution (2.18) as a function of the projected parameter $E[X] = \int_0^\infty (1-s(x)) dx > 0$.

Before going back to the case of considering the effect of the competition, let us show the instability of the unique equilibrium solution (2.18) by means of a linearization procedure in an infinite dimensional setting. Indeed, we are going to apply the principle of linearized (in)stability stated by M. Iannelli in [53] chapter IV. So, we have to linearize system (2.17) in a neighbourhood of the equilibrium and then to compute the so-called *characteristic equation*.

First of all, notice that the no-competition system (2.17) is under the assumptions of the general non-linear model investigated in [53] chapter III, which however does not explicitly take sexual reproduction into account. Indeed, let $a_+ := \infty$ be the maximum age, let $I_2(t) = \int_0^\infty s(x)u(x,t) dx$ and $I_3(t) = \int_0^\infty \gamma_0(x)s(x)u(x,t) dx \leq \|\gamma_0\|_\infty I_2(t)$ be two weighted population sizes, and let

$$\bar{\beta}(a, I_2, I_3) := \frac{\beta_0(a)(1-s(a))I_3}{1+hI_2} \leq \frac{\|\beta_0\|_\infty \|\gamma_0\|_\infty}{h} \quad \text{and} \quad \bar{\mu}(a, I_2, I_3) := \mu(a, 0) \geq \mu_0$$

be the age-specific and density-dependent fertility and mortality, respectively, appearing in the non-linear model of [53]. Now we see that the assumptions (on local integrability with respect to age, boundedness, Lipschitz continuity with respect to the I_2, I_3 , and differentiability with respect to the I_2, I_3) required in chapter III and IV of [53], are fulfilled for this concrete form of the vital rates. We remark that indices 2 and 3 above are taken to agree with the notation of Section 2.4.1.

Let us linearize system (2.17) in a neighbourhood of the unique steady state (2.18). So, we must linearize the birth function \mathcal{B}_0 which in system (2.17) is understood as a (non-linear) functional on L^1 . By the Taylor expansion of the birth function \mathcal{B}_0 around u^* , for $\phi \in L^1$ such

that $\|\phi\|_1$ is small enough, one has that:

$$\begin{aligned} \mathcal{B}_0((1-s)(u^* + \phi), s(u^* + \phi)) &= \mathcal{B}_0((1-s)u^*, su^*) + \langle \beta_0, (1-s)\phi \rangle \frac{\|\gamma_0 su^*\|_1}{1+h\|su^*\|_1} + \\ &+ \|\beta_0(1-s)u^*\|_1 \frac{\langle \gamma_0, s\phi \rangle}{1+h\|su^*\|_1} - \|\beta_0(1-s)u^*\|_1 \frac{\|\gamma_0 su^*\|_1 h \langle 1, s\phi \rangle}{(1+h\|su^*\|_1)^2} + \dots \end{aligned}$$

Now we can simplify this expansion substituting u^* for its expression given in (2.18), i.e.

$$\begin{aligned} \mathcal{B}_0((1-s)(u^* + \phi), s(u^* + \phi)) &= \mathcal{B}_0((1-s)u^*, su^*) + \\ &+ \frac{\langle \beta_0, (1-s)\phi \rangle}{\|\beta_0(1-s)\Pi_0\|_1} + \frac{\langle \gamma_0, s\phi \rangle}{\|\gamma_0 s\Pi_0\|_1} - \frac{h \langle 1, s\phi \rangle}{\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s\Pi_0\|_1} + \dots \end{aligned} \quad (2.19)$$

So, the linearized system is obtained from (2.17) substituting \mathcal{B}_0 by the three linear terms of its Taylor expansion given in (2.19), i.e.

$$\bar{u}(a, t) = \begin{cases} \bar{u}^0(a-t) \frac{\Pi_0(a)}{\Pi_0(a-t)} & \text{a.e. } a \geq t \\ \left(\frac{\langle \beta_0, (1-s)\bar{u}(\cdot, t-a) \rangle}{\|\beta_0(1-s)\Pi_0\|_1} + \frac{\langle \gamma_0, s\bar{u}(\cdot, t-a) \rangle}{\|\gamma_0 s\Pi_0\|_1} - \frac{h \langle 1, s\bar{u}(\cdot, t-a) \rangle}{\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s\Pi_0\|_1} \right) \Pi_0(a) & \text{a.e. } a < t \end{cases} \quad (2.20)$$

The asymptotic behaviour of the solutions of the linearized system (2.20) is given by the so-called *persistent solutions*, i.e. solutions of the form $\bar{u}(a, t) = c e^{\lambda(t-a)} \Pi_0(a)$, $a, t \geq 0$, where c is an arbitrary constant and $\lambda \in \mathbb{C}$, the eigenvalues, satisfy the characteristic equation:

$$1 = \frac{\langle \beta_0, e^{-\lambda \cdot} (1-s)\Pi_0 \rangle}{\|\beta_0(1-s)\Pi_0\|_1} + \frac{\langle \gamma_0, e^{-\lambda \cdot} s\Pi_0 \rangle}{\|\gamma_0 s\Pi_0\|_1} - \frac{h \langle 1, e^{-\lambda \cdot} s\Pi_0 \rangle}{\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s\Pi_0\|_1}, \quad (2.21)$$

with an additional condition, namely, $\text{Re}(\lambda) > -\mu_0$ in order to guarantee that $\bar{u}(\cdot, t)$ belongs to L^1 . If the population density takes the form $\bar{u}(a, t) = c e^{\lambda(t-a)} \Pi_0(a)$, one says that the population exhibits balanced or asynchronous exponential growth.

The characteristic equation (2.21) is obtained from the boundary condition ($a = 0$) of the linearized system (2.20), using the form of the persistent solutions. This is just a simple way of computing the characteristic equation. Actually, the characteristic equation can be obtained in general by equating the determinant of a certain matrix, to zero (see for instance [74] or [53]). See also [46] for the existence of a strictly dominant eigenvalue determining the asymptotic behaviour of solutions of classical linear age-dependent population models, using Perron-Frobenius techniques.

Next theorem states that whenever the equilibrium solution exists, it must be unstable.

Theorem 2.9 (no-competition). *The system (2.17) has at most a non-trivial steady state, which exists if and only if the parameters $s(\cdot), \beta_0(\cdot), \gamma_0(\cdot), h$ and $\mu(\cdot, 0)$ satisfy the condition $(\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s \Pi_0\|_1 - h \|s \Pi_0\|_1) > 0$, where $\Pi_0(a) := e^{-\int_0^a \mu(y, 0) dy}$, $a \geq 0$. Furthermore, the non-trivial steady state, explicitly given in (2.18), is unstable whenever it exists.*

Proof. To end up it suffices to show that there exists a real positive eigenvalue, i.e. a positive root of the characteristic equation (2.21). Indeed, it is enough regarding the right hand side of (2.21) as a function of real variable λ ,

$$g(\lambda) := \frac{\|\beta_0 e^{-\lambda \cdot} (1-s)\Pi_0\|_1}{\|\beta_0(1-s)\Pi_0\|_1} + \frac{\|\gamma_0 e^{-\lambda \cdot} s \Pi_0\|_1}{\|\gamma_0 s \Pi_0\|_1} - \frac{h \|e^{-\lambda \cdot} s \Pi_0\|_1}{\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s \Pi_0\|_1}.$$

Function $g(\lambda)$ is continuous, $g(0) > 1$ since $g(0) = 2 - \frac{h \|s \Pi_0\|_1}{\|\beta_0(1-s)\Pi_0\|_1 \|\gamma_0 s \Pi_0\|_1} > 1$ which is a direct consequence of the hypothesis on the parameters, and $\lim_{\lambda \rightarrow \infty} g(\lambda) = 0$ because each term in the definition of $g(\lambda)$ tends to zero. So, by the intermediate value theorem there exists $\bar{\lambda} > 0$ such that $1 = g(\bar{\lambda})$, i.e. $\bar{\lambda} > 0$ is a real solution to the characteristic equation (2.21).

Finally, applying THEOREM 3.2 in [53] chapter IV, the statement follows, that is, the non-trivial stationary solution of the no-competition system (2.17) is unstable. \square

2.6.2 A case with competition

In this section we are going to illustrate by means of a quite large family of model parameters, the *steady state curve* of the reduced system (2.9), which arises as the expected critical age $E[X]$ is varied. The idea is to use the known results on the system neglecting competition, see the previous section, in order to find non-trivial equilibria of system (2.9) when considering some sort of competition.

Concerning to the transition process between sexes, we address here two paradigmatic situations from the biological point of view, namely, the case of a species such that everybody change sex at the same specific age, and on the other hand, the case of a species such that individuals change sex at different ages but the rate of the transition is constant for all ages. These cases (already mentioned in Section 2.2) correspond to a random critical age X with probability distribution function $s(a) = \mathcal{X}_{[l, \infty)}(a)$ and $s(a) = \int_0^a \frac{e^{-x/l}}{l} dx = 1 - e^{-\frac{a}{l}}$, respectively. Notice that in both cases the expected critical age is explicitly given by the new parameter $l > 0$, i.e. $E[X] = l$.

Concerning to the density-dependence of both fertilities $\beta(a, p)$ and $\gamma(a, p)$ in Hypothesis 2.7 (Holling type II functional response), in addition to the natural assumption of being non-increasing in population size, one biologically reasonable assumption is to consider that the effect of the

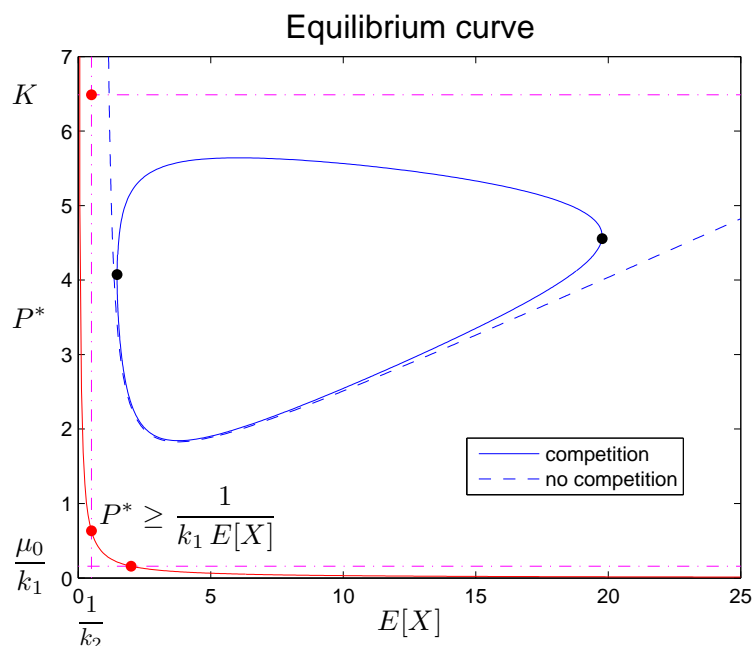


Figure 2.3: The case of an exponential distribution $s(a) = 1 - e^{-\frac{a}{l}}$, $E[X] = l > 0$, i.e. sex-reversal takes place at a constant rate $\frac{1}{l}$ for all ages. Plots in the picture are in total population (the integral over the age span). The trivial equilibrium (*bottom*) is always locally asymptotically stable. The non-trivial equilibrium (*dashed line*) of the no-competition system (2.17), given by (2.18), is unstable. There exist two non-trivial equilibria (*solid line*) of the reduced system (2.9), for each value of the expected critical age $E[X]$ in a bounded open interval, i.e. the closed continuous curve (l, P^*) which is implicitly defined by (2.15). See Sections 2.6.1 and 2.6.2.

competition for the limited resources is relevant at high population densities (say for instance, when $p \geq \bar{b}$) whereas it is (almost) irrelevant at low population densities, i.e. the system behaves very close to the no-competition system (2.17) if the population size is less than a certain threshold (say, when $p < \bar{b}$).

For practical purposes, we will take a mortality rate to be age independent and increasing in population size.

So, let us consider the reduced system (2.9) again, and let us introduce a specific form for the vital parameters of the population describing the situation depicted above: let $\alpha, \alpha_1, \alpha_2 > 0$ and

$b, \bar{b}, c, \bar{c} > 0$ be positive constants, then we define

$$\begin{aligned}\mu(a, p) &:= \mu_0 + \mu_1 (1 - e^{-\alpha p}) \geq \mu_0, \\ \beta(a, p) &:= \frac{1}{2} \left(1 - \tanh(b(p - \bar{b}))\right) (b_0 + b_2 a e^{-\alpha_1 a}) \geq 0, \text{ and} \\ 0 \leq \gamma(a, p) &:= \frac{1}{2} \left(1 - \tanh(c(p - \bar{c}))\right) (c_0 + c_2 a e^{-\alpha_2 a}) \leq 1.\end{aligned}$$

Notice that both fertilities have a *sigmoid decay*, i.e. inverted-S-shaped function, with respect to the population size p . Recall that the birth function in system (2.9) is the following non-linear functional on L^1 :

$$\phi \mapsto \mathcal{B}((1-s)\phi, s\phi) = \langle \beta(\cdot, \mathcal{P}), (1-s)\phi \rangle \frac{\langle \gamma(\cdot, \mathcal{P}), s\phi \rangle}{1 + h \langle 1, s\phi \rangle}, \quad \mathcal{P} := \langle 1, \phi \rangle.$$

Here, the constants k_1 and k_2 , related to the upper bounds of the influx of the newborns (see Hyp. 2.2), turn out to be $k_1 = \max\{b_0, b_0 + \frac{b_2}{\alpha_1 e}\} \times \max\{c_0, c_0 + \frac{c_2}{\alpha_2 e}\} > 0$ and $k_2 = \frac{k_1}{h} > 0$. We also recall that we are assuming that the inequality $\mu_0 < k_2$ holds and that the constant K in the condition assuring bounded trajectories (2.12) is such that $\frac{\mu_0}{k_1} < K$. Here, K is given by the unique positive solution $p = K > 0$ of the scalar non-linear equation

$$\frac{1}{4} \left(1 - \tanh(b(p - \bar{b}))\right) \left(1 - \tanh(c(p - \bar{c}))\right) k_2 - (\mu_0 + \mu_1 (1 - e^{-\alpha p})) = 0.$$

Indeed, the left hand side above is a decreasing function in p which is positive at zero (for \bar{b} and \bar{c} large enough) and negative at infinity.

Finally, taking a combination of values of the parameters such that the unstable steady state of the no-competition system (2.17) exists, see Theorem 2.9, we have found the results shown in Figures 2.2 and 2.3.

Summarizing, we have investigated the equilibrium curve of system (2.9) while varying the expected critical age, i.e. the curve in the (l, P^*) -plane implicitly defined by equation (2.15), for several values of the constants in the parameters μ, β and γ according to the specific form given above, always obtaining the same qualitative picture: a closed continuous curve homeomorphic to \mathcal{S}^1 .

So, under the assumptions of this section, we have found two non-trivial equilibria of the reduced system (2.9) for each value of the expected critical age $E[X] = l$ in some bounded open interval.

Both Figures 2.2 and 2.3, regarded as bifurcation diagrams, also illustrate the fact that the branch of non-trivial equilibria does not intersect the branch of trivial solutions, which means that

in the present model we have assumed a full Allee effect. However, the bifurcation of a branch of non-trivial equilibria from the trivial one occurs very often in population dynamics, see e.g. [40] section 2.

2.7 Linear stability analysis

In this section we are going to study the local stability of non-trivial equilibria u^* of the reduced system (2.9), which are given by the formula (2.13) for each positive solution of equation (2.15), by means of a linearization procedure in an infinite dimensional setting.

The stability of equilibria is usually achieved by both showing that the so-called *growth bound* of an associated semigroup of linear operators is negative, and proving a suitable *principle of linearized stability*. The former is related to the *spectral bound*, i.e. the supremum of the real parts of the spectrum of the infinitesimal generator (see [62] and [74]). The latter means that we must establish a relationship between the stability of the equilibrium states and the stability of the linearized system.

For a proof of the principle of linearized stability for the reduced system (2.9), see Appendix A. This result, which is stated in Theorem A.8 at the end of the appendix, is based on a general principle of linearized stability for a class of non-linear evolution equations involving accretive operators in Banach spaces, see Theorem A.1 at the beginning of the appendix, or theorems 2.1 and 3.1 and corollary 3.2 in the paper by W.M. Ruess [68]. See also [55]. Let us point out that accretive operators were introduced independently in 1967 by F.E. Browder [17] and T. Kato [54], as an extension of the well-known class of monotone operators in Hilbert spaces. For the definitions and properties of accretive operators and m -accretive operators see for instance the book by V. Barbu [11].

So, let us consider the reduced system (2.9) as an abstract Cauchy problem in L^1 , namely, the following non-linear evolution equation (for the age-density $u(t) \equiv u(\cdot, t)$):

$$\begin{cases} \frac{\partial}{\partial t} u(t) + \left(\frac{\partial}{\partial a} + \omega \right) u(t) = \left(\omega - \mu(\cdot, \int_0^\infty u(t) dx) \right) u(t), & t \geq 0, \\ u(t) |_{a=0} = \mathbf{B}(u(t)) := \mathcal{B}((1-s)u(t), s u(t)), & t \geq 0, \\ u(0) = u^0 \in L^1. \end{cases} \quad (2.22)$$

In addition to Hypotheses 2.1 – 2.7, let us assume the (technical) Hypotheses A.1 – A.4 and $\omega \geq C_1$, that is to say: there exists a non-trivial equilibrium u^* of (2.22) which belongs to the Sobolev space $W^{1,1}(0, \infty; \mathbb{R})$ (in particular, is an absolutely continuous function), the

non-linear functional \mathbf{B} (the birth function in (2.22)) is continuously Fréchet-differentiable in an open neighbourhood of the equilibrium and it is also globally Lipschitz continuous with constant $C_1 > 0$, and the age-specific and density-dependent mortality rate $\mu(a, p)$ is such that the functions $a \mapsto \mu(a, 0)$ and $a \mapsto D_2\mu(a, \int_0^\infty u^* dx)$ are essentially bounded, where D_2 stands for the derivative with respect to the second variable. For further details see Appendix A.

The linearization of system (2.22) in a neighbourhood of an equilibrium u^* , taking formally $u(t) \simeq u^* + v(t)$, turns out to be

$$\begin{cases} \frac{\partial}{\partial t} v(t) + \left(\frac{\partial}{\partial a} + \omega\right) v(t) = \left(\omega - \mu(\cdot, \int_0^\infty u^* dx)\right) v(t) - D_2\mu(\cdot, \int_0^\infty u^* dx) u^* \int_0^\infty v(t) dx, & t \geq 0, \\ v(t)|_{a=0} = \langle \mathbf{B}'(u^*), v(t) \rangle, & t \geq 0, \\ v(0) = v^0 \in L^1, \end{cases} \quad (2.23)$$

that is, using the Taylor expansion around u^* of the non-linear terms in system (2.22) we get the linearized system (2.23).

Now applying Theorem A.8, stated at the end of Appendix A, we have that u^* is a locally exponentially stable non-trivial steady state if the ‘linearized’ operator $(\tilde{A} - \tilde{F} - \tilde{\omega} I)$ is accretive for some $\tilde{\omega} > 0$, where the linear operator \tilde{A} and the bounded linear operator \tilde{F} are defined in (A.7) and (A.10) respectively, and I is the identity operator in L^1 . These latter operators are related to the linearized system (2.23), and for the sake of completeness we recall that $\tilde{A} : \mathcal{D}(\tilde{A}) \subset L^1 \rightarrow L^1$ is defined by:

$$\begin{cases} \tilde{A}\phi = \phi' + \omega\phi \\ \mathcal{D}(\tilde{A}) = \{\phi \in W^{1,1} : \phi(0) = \langle \mathbf{B}'(u^*), \phi \rangle\}, \end{cases} \quad (2.24)$$

and $\tilde{F} : L^1 \rightarrow L^1$ is defined by:

$$\tilde{F}\phi = \left(\omega - \mu(\cdot, \int_0^\infty u^* dx)\right)\phi - D_2\mu(\cdot, \int_0^\infty u^* dx) u^* \int_0^\infty \phi dx. \quad (2.25)$$

We also recall that a (general) single-valued operator A is said to be accretive in L^1 if

$$\langle \text{sign}(\phi - \bar{\phi}), A\phi - A\bar{\phi} \rangle \geq 0, \quad \text{for each pair } \phi, \bar{\phi} \text{ in the domain of } A.$$

So, in our case, in order to show the accretiveness of the linear operator $(\tilde{A} - \tilde{F} - \tilde{\omega} I)$ it suffices to show that

$$\langle \text{sign}(\phi), (\tilde{A} - \tilde{F} - \tilde{\omega} I)\phi \rangle \geq 0, \quad \text{for each } \phi \in \mathcal{D}(\tilde{A}). \quad (2.26)$$

Now, a sufficient condition for the local stability can be derived as follows. From (2.24) and (2.25), and proceeding as in the Appendix A, we have that for each $\phi \in \mathcal{D}(\tilde{A})$,

$$\begin{aligned} \langle \text{sign}(\phi), (\tilde{A} - \tilde{F} - \tilde{\omega} I) \phi \rangle &= \langle \text{sign}(\phi), \phi' + (\mu(\cdot, \int_0^\infty u^* dx) - \tilde{\omega}) \phi + D_2\mu(\cdot, \int_0^\infty u^* dx) u^* \int_0^\infty \phi dx \rangle \\ &= \int_0^\infty \left(|\phi(a)|' + (\mu(a, \int_0^\infty u^* dx) - \tilde{\omega}) |\phi(a)| + \text{sign}(\phi)(a) D_2\mu(a, \int_0^\infty u^* dx) u^*(a) \int_0^\infty \phi dx \right) da \\ &= -|\phi(0)| + \int_0^\infty (\mu(a, P^*) - \tilde{\omega}) |\phi(a)| da + \int_0^\infty \text{sign}(\phi)(a) D_2\mu(a, P^*) u^*(a) da \int_0^\infty \phi(x) dx \\ &\geq -|\langle \mathbf{B}'(u^*), \phi \rangle| + (\underline{\mu}(P^*) - \tilde{\omega}) \|\phi\|_1 - \|D_2\mu(\cdot, P^*)\|_\infty P^* \|\phi\|_1 \\ &\geq (-\|\mathbf{B}'(u^*)\|_\infty + \underline{\mu}(P^*) - \tilde{\omega} - \|D_2\mu(\cdot, P^*)\|_\infty P^*) \|\phi\|_1. \end{aligned}$$

Therefore, if u^* is a non-trivial steady state of system (2.22), with $P^* = \int_0^\infty u^*(x) dx$ being the total population at equilibrium, such that the following condition

$$(\underline{\mu}(P^*) - \|\mathbf{B}'(u^*)\|_\infty - \|D_2\mu(\cdot, P^*)\|_\infty P^*) > 0 \quad (2.27)$$

holds, then u^* is a locally exponentially stable non-trivial steady state. Indeed, (2.27) is a sufficient condition assuring (2.26) for some $\tilde{\omega} > 0$, and therefore by Theorem A.8 the statement follows.

Notice that, thanks to the theory developed in Appendix A, the local stability of the equilibria can be determined without computing the spectrum of the associated linear operator $-(\tilde{A} - \tilde{F})$, since we just have to show the accretiveness of the related linear operator $(\tilde{A} - \tilde{F} - \tilde{\omega} I)$, $\tilde{\omega} > 0$, see above. However, (2.27) is a sufficient condition for the stability and then it will not be optimum in general.

Finally, let us point out that, unfortunately, Theorem A.8 does not give any criteria for the instability of the equilibria.

2.8 Evolutionary dynamics of critical age

So far we have studied the *ecological dynamics* of the present model of sequential hermaphroditism, taking all the parameters in the model as ‘immutable’, let us say, given or prescribed. Now we turn our interest into some aspects concerning with *biological evolution* in the model.

Considering phenotypic evolution in the context of diploid population models incorporating interactions among individuals due to competition and sexual reproduction, we address the question of how *sex-reversal* evolves by the combined action of *random mutation* and *natural selection*. The former introduces genetic differences among individuals of the population, which have to be

physically observable through a phenotypic characteristic, whereas the latter is understood as a natural process “acting” on the phenotypic variability.

So, we undertake here a study of the *evolutionary dynamics* or *adaptive dynamics* of the probability distribution function (pdf) of the age at sex-reversal $s(a)$, $a \geq 0$, which turns out to be a function-valued evolutionary trait of the population. So, the trait is neither a scalar-valued parameter nor a finite dimensional vector-valued parameter but a function of the individuals age. For a similar analysis, see e.g. [25] where the authors consider an energy allocation function as (infinite-dimensional) evolutionary trait in a non-linear continuously size-structured population model coupled with a dynamic resource. For an example of a multi-dimensional evolutionary trait in a hierarchical non-linear discrete population model with a general transition matrix, see e.g. [66]. In loc. cit., the authors undertake a study of the adaptive dynamics of a vector of transition probabilities among classes of individuals.

A particular value of an evolutionary trait is called *type* or, more generally, *strategy*. In this section we will show, using convex analysis, that the pdf of the critical age which turns out to be an unbeatable strategy or evolutionarily stable strategy (ESS, in the sense of [59]) is a particular Heaviside step function (see below). Therefore, the ‘*best*’ evolutionary success is attained when sex-reversal takes place only at a single specific age. Consequently, we will find indirectly the *adaptive value* of the sex-ratio of the population at equilibrium.

For a discussion on the evolution of sex-reversal (and also on the evolution of sex-ratio in general) see for instance E.L. Charnov [32] and [33].

For a nice introduction to adaptive dynamics see for instance O. Diekmann in [67] and the references therein, specially the paper [45] where a classification of singular points of the adaptive dynamics (i.e. where the selection gradient vanishes) for one-dimensional evolutionary traits is given. These points are sometimes referred to as *evolutionarily singular strategies*.

In this section, we consider that the function-valued parameter $s : [0, \infty) \rightarrow [0, 1]$ appearing in systems (2.5) and (2.9), the latter being the reduced version of the former, corresponds to an inheritable life-history characteristic of the population which is genetically determined and it is susceptible of random mutations (i.e. random changes in the genetic make-up of individuals occur). We keep the remaining parameters, β, γ, h and μ , as given/prescribed. We recall that we are assuming Hypotheses 2.1 – 2.7.

The fact of having considered the ecological dynamics (i.e. the evolution in the number and composition of individuals of the population) separately from the adaptive dynamics (i.e. the trait/strategy substitution sequence), corresponds with the usual hypothesis of the separation of time scales, i.e. the mutation process occurs on a time scale which is long relative to the time scale

of convergence to an ecological attractor (e.g. an asymptotically stable ecological equilibrium). So, both dynamics can be uncoupled one from each other.

The modern theory of adaptive dynamics, as initiated by J.A.J. Metz et al. in 1992, stems from *game theory*. J. Maynard-Smith, one of the most renowned and influential evolutionary biologists, applied game theory to interactions between competing individuals of a single species that use different strategies for survival. In his book [58] “Evolution and the Theory of Games”, he described the concept of an *evolutionarily stable strategy* (ESS), which it was first introduced by Maynard-Smith and Price in 1973, see [59]. Roughly speaking, an ESS is a strategy that, if adopted by the vast majority of the individuals in a population, will resist invasion by individuals with a new (different) strategy. The adaptive dynamics framework can be seen as a dynamic extension of ESS theory, where an ESS is simply a *monomorphic* steady strategy for the adaptive dynamics which may be either an evolutionary attractor or an evolutionary repeller. The decisive criterion for the evolutionary success or failure of a (small) invading/mutant population is its rate of spread (i.e. its long term population growth rate) in the environmental conditions set by the current established (or resident) population. This is the so-called *linear invasibility test* and guarantees failure if the rate of spread is negative, whereas it *predicts* success if the rate of spread is positive. If we take for granted that a successful invasion results in take-over, i.e. leads to the extinction of the resident population, then a trait substitution will occur. Accordingly, an ESS is defined as a fixed point of this trait/strategy substitution sequence, i.e. a strategy such that, when it is adopted by the resident population, leads to the evolutionary failure of any (small) mutant population.

2.8.1 Diploid inheritance

First of all, let us point out that the adaptive dynamics theory usually assumes clonal reproduction, i.e. offspring are genetically identical to the parent, but this is not possible here due to the sexual reproduction. Instead, we have to consider diploid inheritance.

The starting point to study the evolutionary dynamics of the pdf of the critical age is to assume genetic differences among individuals of the population expressing different choices of the pdf. To this end, let us consider a sequential hermaphrodite (diploid) population like the one described in Section 2.1 (in particular recall that we have assumed random mating), and let us suppose that individuals are distinguished not only on the basis of their sex and age but also on the basis of their genotype $\{aa, aA, AA\}$, the latter being a single-locus two-alleles diploid system. In our case, the genotype is physically (phenotypically) expressed/displayed through

a particular probability distribution function of the age at sex-reversal (a non-negative random variable). On the one hand, we refer to the individuals with genotype aa as resident homozygotes, who change sex according to a pdf denoted by $s(a)$, $a \geq 0$. As in Section 2.2, we suppose an upper threshold age $\sup\{a : s(a) < 1\} =: a_1 > 0$, or equivalently $s(0) < 1$, which is a necessary condition for the existence of a non-trivial equilibrium. On the other hand, we refer to the individuals with genotype aA and genotype AA as invading/mutant heterozygotes and invading/mutant homozygotes respectively, both changing sex according to a new pdf denoted by $s_i(a)$, $a \geq 0$ (where the “i” stands for invader). Here we take for granted that the mutant allele A is dominant, so, $s(a)$ and $s_i(a)$ are the resident and invading/mutant phenotypes respectively.

Hence, the resulting system is a (genotype, sex and age)-structured population dynamics model with six state variables which correspond to the six subclasses of individuals of the population, namely, the (time dependent) densities with respect to age of females and males for each genotype: $f_{aa}, m_{aa}, f_{aA}, m_{aA}, f_{AA}, m_{AA}$, which we think as non-negative functions. The full non-linear system describing the dynamics of such a population, can be written as three coupled systems where each one has the form of the non-reduced system (2.5) but with a birth function resulting from the diploid inheritance for each genotype (see below), and a survival probability depending on the whole total population (i.e. the integral over the age span of the addition of the six classes).

Concerning with the birth process, let us rewrite \mathcal{B} , the birth function defined in Hypothesis 2.7, in a more suitable way from the modelling point of view. So, let $\mathcal{B}_I : L^1 \times L^1 \rightarrow \mathbb{R}$ be a bilinear functional defined as

$$\mathcal{B}_I(\phi, \psi) := \langle \beta(\cdot, I_1), \phi \rangle \frac{\langle \gamma(\cdot, I_1), \psi \rangle}{1 + h I_2}, \quad I = (I_1, I_2) \in \mathbb{R}^2,$$

where I is a two-dimensional vector describing the environmental conditions as far as individuals are influenced by interaction. Notice that $|\mathcal{B}_I(\phi, \psi)| \leq \frac{\|\beta(\cdot, I_1)\|_\infty \|\gamma(\cdot, I_1)\|_\infty}{|1 + h I_2|} \|\phi\|_1 \|\psi\|_1$. If we take the vector of interaction variables to be $I = (\langle 1, \phi + \psi \rangle, \langle 1, \psi \rangle)$ then we obtain the original birth function $\mathcal{B}(\phi, \psi) = \mathcal{B}_I(\phi, \psi)$.

On the other hand, a straightforward application of the Mendel rules to a (general) diploid population gives the map genotype \times genotype \rightarrow genotype, which we have summarized in Table 2.2. So, the birth rates of each subclass of individuals are given according to the possible genetic combinations. Using the bilinear functional \mathcal{B}_I and the coefficients in each row of the Table 2.2 we can compute each birth rate. Indeed, the birth rate of the resident homozygotes (of both sexes) is computed as

$$\mathcal{B}_I(f_{aa}, m_{aa}) + \frac{1}{2} \mathcal{B}_I(f_{aa}, m_{aA}) + \frac{1}{2} \mathcal{B}_I(f_{aA}, m_{aa}) + \frac{1}{4} \mathcal{B}_I(f_{aA}, m_{aA}), \quad (2.28)$$

	f_{aa} × m_{aa}	f_{aA} × m_{aA}	f_{AA} × m_{AA}	f_{aa} × m_{aa}	f_{aA} × m_{aA}	f_{aA} × m_{AA}	f_{AA} × m_{aa}	f_{AA} × m_{aA}	f_{AA} × m_{AA}
aa	1	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{4}$	0	0	0	0
aA	0	$\frac{1}{2}$	1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	1	$\frac{1}{2}$	0
AA	0	0	0	0	$\frac{1}{4}$	$\frac{1}{2}$	0	$\frac{1}{2}$	1

Table 2.2: Diploid inheritance in a one-locus two-alleles system $\{aa, aA, AA\}$. Each column of the table corresponds with the proportions of the three different genotypes among the newborn individuals, with regard to the genotypes of their parents (female × male). The coefficients are derived from the Mendel rules.

the birth rate of the invading/mutant heterozygotes (of both sexes) equals to

$$\begin{aligned} & \frac{1}{2} \mathcal{B}_I(f_{aa}, m_{aA}) + \mathcal{B}_I(f_{aa}, m_{AA}) + \frac{1}{2} \mathcal{B}_I(f_{aA}, m_{aa}) + \frac{1}{2} \mathcal{B}_I(f_{aA}, m_{aA}) + \\ & + \frac{1}{2} \mathcal{B}_I(f_{aA}, m_{AA}) + \mathcal{B}_I(f_{AA}, m_{aa}) + \frac{1}{2} \mathcal{B}_I(f_{AA}, m_{aA}), \end{aligned} \quad (2.29)$$

and finally the birth rate of the invading/mutant homozygotes (of both sexes) is given by

$$\frac{1}{4} \mathcal{B}_I(f_{aA}, m_{aA}) + \frac{1}{2} \mathcal{B}_I(f_{aA}, m_{AA}) + \frac{1}{2} \mathcal{B}_I(f_{AA}, m_{aA}) + \mathcal{B}_I(f_{AA}, m_{AA}), \quad (2.30)$$

where, in all cases, the interaction variables $I = (I_1, I_2)$ are given by the whole total population and whole total male population, respectively. Using the bilinearity of the functional \mathcal{B}_I , it is routine to check that the sum of the three birth rates (2.28)–(2.30) equals to the whole birth rate, i.e. $\mathcal{B}_I(f_{aa} + \frac{f_{aA}}{2}, m_{aa} + \frac{m_{aA}}{2}) + (\mathcal{B}_I(f_{aa} + \frac{f_{aA}}{2}, m_{AA} + \frac{m_{aA}}{2}) + \mathcal{B}_I(f_{AA} + \frac{f_{aA}}{2}, m_{aa} + \frac{m_{aA}}{2})) + \mathcal{B}_I(f_{AA} + \frac{f_{aA}}{2}, m_{AA} + \frac{m_{aA}}{2}) = \mathcal{B}_I(f_{aa} + f_{aA} + f_{AA}, m_{aa} + m_{aA} + m_{AA})$.

Let $f_{aa}^0(a)$, $m_{aa}^0(a)$ and $f_{aA}^0(a)$, $m_{aA}^0(a)$, $f_{AA}^0(a)$, $m_{AA}^0(a)$ be the known non-negative initial age distributions which are biologically meaningful for the present model, according to $s(a)$ and $s_i(a)$ respectively, see the definitions in (2.1) and Hypothesis 2.4 in Section 2.2.

Let us assume that the resident homozygotes (f_{aa}, m_{aa}) have reached a locally asymptotically stable non-trivial steady state in the absence of both mutant populations (a locally asymptotically stable non-trivial equilibrium of the non-reduced ecological system (2.5)), i.e.

$$\left(f^*(a), m^*(a) \right) = \left((1 - s(a)) u^*(a), s(a) u^*(a) \right) \quad \text{with} \quad u^*(a) = \frac{P^*}{\|\Pi_*\|_1} \Pi_*(a), \quad a \geq 0, \quad (2.31)$$

where $P^* > 0$ is a solution of the scalar non-linear equation (2.15) such that, for instance, the sufficient condition of local stability (2.27) holds. The latter is a consequence of the fact that the dynamics of the resident population alone is given by the complete system (2.5), which in its turn can be completely determined by the reduced system (2.9) (or (2.22) which is the reduced system seen as an evolution equation in L^1). See Sections 2.4, 2.6 and 2.7.

Next, let us introduce a rare mutant population, i.e. individuals of both genotypes aA and AA such that its population size is small relative to the population size of the resident homozygotes at equilibrium. In this situation, we can carry out the so-called linear invasibility test, which is based on the analysis of the linear dynamics in a neighbourhood of the non-trivial steady state $(f^*(a), m^*(a), 0, 0, 0, 0)$, $a \geq 0$, of the full non-linear system (*resident- aA invader- AA invader*).

So, the vital parameters of the population in an environmental conditions set by the current resident (at stable equilibrium), can be taken as:

$$\begin{aligned} \beta_*(a) := \beta(a, P^*) \geq 0, \quad 0 \leq \gamma_*(a) := \gamma(a, P^*) \leq 1, \quad \mathcal{B}_{I_*}(\phi, \psi) = \langle \beta_*, \phi \rangle \frac{\langle \gamma_*, \psi \rangle}{1+h \|su^*\|_1}, \\ \text{and } 0 < \Pi_*(a) = e^{-\int_0^a \mu(y, P^*) dy} \leq 1. \end{aligned} \quad (2.32)$$

It is worth to mention that here the steady environmental interaction variables are given by $I_* := (\|f^* + m^*\|_1, \|m^*\|_1) = (P^*, \|su^*\|_1) = (\int_0^\infty u^*(x) dx, \int_0^\infty s(x) u^*(x) dx)$.

The linear approximation of the birth rate of resident homozygotes (2.28) is given by

$$(\mathcal{B}_{I_*}(f^*, m^*) + \mathcal{L}^*(\bar{f}_{aa}, \bar{m}_{aa})) + \frac{1}{2}(\mathcal{B}_{I_*}(f^*, m_{aA}) + \mathcal{B}_{I_*}(f_{aA}, m^*))$$

where \mathcal{L}^* stands for the linearized birth rate of the resident population at the (stable) equilibrium (f^*, m^*) , whereas the linear approximation of the birth rate of mutant heterozygotes (2.29) is $\frac{1}{2}(\mathcal{B}_{I_*}(f^*, m_{aA}) + \mathcal{B}_{I_*}(f_{aA}, m^*)) + (\mathcal{B}_{I_*}(f^*, m_{AA}) + \mathcal{B}_{I_*}(f_{AA}, m^*))$.

On the other hand, the linear approximation of the birth rate of the mutant homozygotes (2.30) gives zero, so its (uncoupled) linear dynamics can be computed explicitly and in particular implies that $0 \leq \|f_{AA}(\cdot, t) + m_{AA}(\cdot, t)\|_1 \leq \|f_{AA}^0 + m_{AA}^0\|_1 e^{-\mu_0 t} \xrightarrow{t \rightarrow \infty} 0$, which means that the mutant homozygous population goes exponentially to extinction. The latter is a general feature of this sort of linear invasibility tests, since practically all mutants come as heterozygotes.

Therefore, the linearized birth rate of the mutant heterozygotes (f_{aA}, m_{aA}) at time t becomes

$$\frac{1}{2}(\mathcal{B}_{I_*}(f^*, m_{aA}(\cdot, t)) + \mathcal{B}_{I_*}(f_{aA}(\cdot, t), m^*)) + b(t),$$

where the second term is a known exponentially small influx of newborns coming from the parents of the other two genotypes, i.e. $0 \leq b(t) := (\mathcal{B}_{I_*}(f^*, m_{AA}(\cdot, t)) + \mathcal{B}_{I_*}(f_{AA}(\cdot, t), m^*)) \leq C e^{-\mu_0 t}$, for

some positive constant C . It can be shown that the stability of the linear system for both mutants $(f_{aA}, m_{aA}, f_{AA}, m_{AA})$ is guaranteed by the stability of the resulting (uncoupled) linear system for the mutant heterozygotes alone (f_{aA}, m_{aA}) dropping the term $b(t)$ in the birth rate above. Indeed, the linear dynamics of mutant heterozygotes is determined by a Volterra integral equation of the second kind for the birth rate, i.e. the following *renewal equation*¹⁰: $B(t) = \mathcal{L}B(t) + B_0(t) + b(t)$, where \mathcal{L} is a bounded linear operator with norm less than one (stability condition), the term $B_0(t)$ is related to the initial age distribution, and the term $b(t)$ is exponentially small. Formally, one has that $B(t) = (I - \mathcal{L})^{-1}(B_0(t) + b(t))$ where I is the identity operator, and the asymptotic behaviour turns out to be $\lim_{t \rightarrow \infty} B(t) = (I - \mathcal{L})^{-1}B_0(\infty)$. See for instance [53] appendix II.

Summarizing, with the convention $\frac{f_{aA}^0(a)}{1-s_i(a)} := 0$, a.e. $a > a_1^i$, where a_1^i is the new upper threshold age of the transition process between sexes, the linear dynamics of the mutant heterozygotes can be described by the following simplified (non-reduced) linear system:

$$\begin{pmatrix} f_{aA}(a, t) \\ m_{aA}(a, t) \end{pmatrix} = \begin{cases} \left[f_{aA}^0(a-t) \begin{pmatrix} \frac{1-s_i(a)}{1-s_i(a-t)} \\ \frac{s_i(a)-s_i(a-t)}{1-s_i(a-t)} \end{pmatrix} + m_{aA}^0(a-t) \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right] \frac{\Pi_*(a)}{\Pi_*(a-t)} & a \geq t \\ \frac{1}{2} \left(\mathcal{B}_{I_*}(f^*, m_{aA}(\cdot, t-a)) + \mathcal{B}_{I_*}(f_{aA}(\cdot, t-a), m^*) \right) \begin{pmatrix} 1-s_i(a) \\ s_i(a) \end{pmatrix} \Pi_*(a) & a < t \end{cases} \quad (2.33)$$

Now we can simplify the birth function above, using the expressions in (2.31) and equation (2.15), i.e. reordering

$$\frac{1}{2} \left(\frac{\langle \beta_*, f_{aA}(\cdot, t-a) \rangle}{\|\beta_* (1-s) \Pi_*\|_1} + \frac{\langle \gamma_*, m_{aA}(\cdot, t-a) \rangle}{\|\gamma_* s \Pi_*\|_1} \right).$$

As in Section 2.4, see Corollary 2.6, the reduced linear system (2.33) can be reduced to its intrinsic sex-ratio subspace, namely, $\{(f_{aA}, m_{aA}) : s_i f_{aA} = (1-s_i) m_{aA}\} \subset L^1 \times L^1$, thus finally obtaining a single linear integral equation for the age-density $u_{aA} = f_{aA} + m_{aA}$ of mutant heterozygous individuals (of both sexes):

$$u_{aA}(a, t) = \begin{cases} u_{aA}^0(a-t) \frac{\Pi_*(a)}{\Pi_*(a-t)} & \text{a.e. } a \geq t \\ \frac{1}{2} \left(\frac{\langle \beta_*, (1-s_i) u_{aA}(\cdot, t-a) \rangle}{\|\beta_* (1-s) \Pi_*\|_1} + \frac{\langle \gamma_*, s_i u_{aA}(\cdot, t-a) \rangle}{\|\gamma_* s \Pi_*\|_1} \right) \Pi_*(a) & \text{a.e. } a < t \end{cases} \quad (2.34)$$

¹⁰The usual renewal equation of linear age-dependent population models with a known exponentially small extra term.

As before in Section 2.6.1, the asymptotic behaviour of the solutions of the linear system (2.34) is given by the so-called *persistent solutions*, i.e. solutions of the form $\bar{u}(a, t) = c e^{\lambda(t-a)} \Pi_*(a)$, $a, t \geq 0$, where c is an arbitrary constant and $\lambda \in \mathbb{C}$, the eigenvalues, satisfy the characteristic equation:

$$2 = \frac{\langle \beta_*, e^{-\lambda \cdot} (1 - s_i) \Pi_* \rangle}{\|\beta_* (1 - s) \Pi_*\|_1} + \frac{\langle \gamma_*, e^{-\lambda \cdot} s_i \Pi_* \rangle}{\|\gamma_* s \Pi_*\|_1}, \quad (2.35)$$

with an additional condition, namely, $\text{Re}(\lambda) > -\mu_0$ in order to guarantee that the function $a \mapsto \bar{u}(a, t)$ belongs to L^1 . In the literature, the form of the right hand side of the equation (2.35) at $\lambda = 0$, i.e.

$$\frac{\int_0^\infty \beta_*(x) (1 - s_i(x)) \Pi_*(x) dx}{\int_0^\infty \beta_*(x) (1 - s(x)) \Pi_*(x) dx} + \frac{\int_0^\infty \gamma_*(x) s_i(x) \Pi_*(x) dx}{\int_0^\infty \gamma_*(x) s(x) \Pi_*(x) dx}$$

is referred as the classical Shaw-Mohler formula, see e.g. “ $\frac{\hat{f}}{\bar{f}} + \frac{\hat{m}}{\bar{m}}$ ” in [32], or [40] section 4.2.

As in Section 2.6.1, if the population density takes the form $\bar{u}(a, t) = c e^{\lambda(t-a)} \Pi_*(a)$, one says that the population exhibits balanced or asynchronous exponential growth. See [46] where a Perron-Frobenius theorem in an abstract infinite-dimensional setting is stated, and in particular it is shown the existence of a strictly dominant eigenvalue determining the asymptotic behaviour of solutions of classical linear age-dependent population models.

So, let us consider as *fitness measure* the strictly dominant eigenvalue of the infinitesimal generator associated to the linear problem (2.34), i.e. the unique real solution of the characteristic equation (2.35), see below. In order to use convex optimization (see below) we have to define a suitable space containing the set of probability distribution functions of a non-negative random variable, for instance, let $L_*^1 := L_*^1(0, \infty; \mathbb{R})$ be the weighted L^1 Banach space (of equivalence classes) equipped with the norm $\|\phi\| := \int_0^\infty |\phi(x)| \Pi_*(x) dx \leq \|\phi\|_1$. In this functional framework, a probability distribution function is an equivalence class of L_*^1 which contains a function like the one defined in Hypothesis 2.1 (i.e. a pdf in the usual sense). So, the latter space will be used as an extension of the set of possible/feasible strategies.

Now let us consider the right hand side of the characteristic equation (2.35) restricted to $\lambda \in \mathbb{R}$, and extended to the space L_*^1 , more precisely, let $G : \mathbb{R} \times \mathcal{E} \times L_*^1 \longrightarrow \mathbb{R}$ be a mapping defined as

$$G(\lambda, \phi, \phi_i) := \frac{\langle \beta_*, e^{-\lambda \cdot} (1 - \phi_i) \Pi_* \rangle}{\|\beta_* (1 - \phi) \Pi_*\|_1} + \frac{\langle \gamma_*, e^{-\lambda \cdot} \phi_i \Pi_* \rangle}{\|\gamma_* \phi \Pi_*\|_1}. \quad (2.36)$$

where the set \mathcal{E} is the subset of L_*^1 formed by the s such that equation (2.15) has a positive solution giving a stable equilibrium for the resident population, and β_*, γ_*, Π_* , defined in (2.32), depend on $P^* > 0$ which solves (2.15) for $s = \phi$, so, they depend implicitly on ϕ .

It is worth to mention that the function G is a continuous affine functional with respect to the third variable $\phi_i \in L_*^1$, that is, $\phi_i \mapsto G(\lambda, \phi, \phi_i) - G(\lambda, \phi, 0)$ is a continuous (bounded) linear functional on L_*^1 .

On the other hand, the restriction of G to the strategy of the resident and to the strategy of the invader, namely $G(\lambda, s, s_i)$, turns out to be continuous, positive and monotone decreasing with respect to $\lambda \in \mathbb{R}$, and $\lim_{\lambda \rightarrow \infty} G(\lambda, s, s_i) = 0$ and $\lim_{\lambda \rightarrow -\infty} G(\lambda, s, s_i) = \infty$. Finally, equation (2.35) for real λ , i.e. $2 = G(\lambda, s, s_i)$, implicitly defines the strictly dominant eigenvalue $\lambda(s, s_i)$ which can be seen as a function of the trait/strategy of the resident s and the trait/strategy of the invader s_i . As it is usual in adaptive dynamics, the following two relations hold: if the mutant phenotype is identical to the resident phenotype then $G(0, s, s) = 2$, i.e. $\lambda(s, s) = 0$, and $G(0, s, s_i) < 2$ if and only if $\lambda(s, s_i) < 0$ which is the condition for a mutant population to be selected against. The latter equivalence is a straightforward consequence of the fact that the mapping $\lambda \mapsto G(\lambda, s, s_i)$ is (strictly) decreasing.

Summarizing, the linear invasibility test, which is given by the reduced linear system (2.34), guarantees the evolutionary failure of a (small) mutant population with strategy $s_i(a)$, $a \geq 0$, in the environmental conditions set by a resident population (at stable equilibrium) with strategy $s(a)$, $a \geq 0$, $s(0) < 1$, if the inequality $G(0, s, s_i) < 2$ holds. On the contrary, it predicts the evolutionary success if the opposite strict inequality $G(0, s, s_i) > 2$ holds.

2.8.2 Evolutionarily stable strategy

In order to complete our analysis, let us compute evolutionarily stable strategies (ESS), i.e. strategies of the resident population guaranteeing the failure of any mutant population. According to the biological context depicted in the previous section, an ESS is a probability distribution function $\hat{s}(a)$, $a \geq 0$, $\hat{s}(0) < 1$, such that

$$G(0, \hat{s}, s_i) < G(0, \hat{s}, \hat{s}) = 2 \quad \text{for all pdf } s_i(a), a \geq 0, \text{ different from } \hat{s}(a).$$

Actually, two probability distribution functions in the usual sense are different if they differ at least in a single point (an age). Using the definition of G in (2.36) which stems from the characteristic equation (2.35), the above condition for a pdf \hat{s} to be an ESS is stated more explicitly in standard notation as

$$\frac{\int_0^\infty \beta_*(x) (1 - s_i(x)) \Pi_*(x) dx}{\int_0^\infty \beta_*(x) (1 - \hat{s}(x)) \Pi_*(x) dx} + \frac{\int_0^\infty \gamma_*(x) s_i(x) \Pi_*(x) dx}{\int_0^\infty \gamma_*(x) \hat{s}(x) \Pi_*(x) dx} < 2 \quad \text{for all pdf } s_i \neq \hat{s}, \quad (2.37)$$

where β_*, γ_*, Π_* , see (2.32), depend on $P^* > 0$ (the total resident population at stable equilibrium) which solves the scalar non-linear equation

$$\int_0^\infty (1 + P^* h \hat{s}(x)) \Pi_*(x) dx = P^* \int_0^\infty \beta_*(x) (1 - \hat{s}(x)) \Pi_*(x) dx \int_0^\infty \gamma_*(x) \hat{s}(x) \Pi_*(x) dx, \quad (2.38)$$

i.e., equation (2.15) for $s = \hat{s}$. Recall that a sufficient condition for a non-trivial equilibrium of the ecological system (2.5) to be locally exponentially stable is given in (2.27).

The computation of such a function-valued ESS is based on linear/affine optimization on compact convex sets. First of all, let us recall some well-known definitions and results of convex analysis. See e.g. [3] chapter 5, [14] chapter I, [72] appendix B.3, and [41] chapter 10.

Let X be a real vector space. A subset $C \subset X$ is said to be *convex* if $tx + (1 - t)y \in C$ whenever $0 \leq t \leq 1$ and $x, y \in C$. The intersection of convex sets is convex. Hence any given subset $Y \subset X$ is contained in a smallest convex subset of X , i.e. the convex envelope or *convex hull* of Y . This envelope is empty if Y is empty, otherwise it is given and denoted by

$$\text{co}(Y) = \left\{ x \in X : x = \sum_{i=1}^n t_i x_i, 0 \leq t_i \leq 1, \sum_{i=1}^n t_i = 1, x_i \in Y \right\},$$

where $n = n(x) \in \mathbb{N}$. Let $C \subset X$ be a non-empty convex subset. A non-empty convex subset $E \subset C$ is called a *face* or *extreme subset* of C if $x, y \in C$, $tx + (1 - t)y \in E$ for some $0 < t < 1$ implies that both $x, y \in E$. An element $z \in C$ is called an *extreme point* of C if the singleton $\{z\}$ is an extreme subset of C , that is, the point $z \in C$ is not a proper convex combination of two other points in C . The set of the extreme points of C will be denoted by $\text{ext}(C)$.

We now turn to locally convex Hausdorff spaces X , for instance a Banach space.

Theorem 2.10 (Krein-Milman). *Let C be a non-empty compact convex subset of a locally convex Hausdorff space X , then C is the closure of the convex hull of the set of its extreme points. In symbols, $C = \overline{\text{co}(\text{ext}(C))}$.*

Notice that the Krein-Milman theorem guarantees that any non-empty compact convex subset has at least an extreme point. Continuous affine/linear functionals always attain their maxima and minima on non-empty compact sets. If in addition the set is convex, then these extrema may always be attained at extreme points. Next theorem concerns with the optimization of a continuous affine (in particular linear) functional on a compact convex set.

Theorem 2.11. *Let C be a non-empty compact convex subset of a locally convex Hausdorff space X , let $g : X \rightarrow \mathbb{R}$ be a continuous affine functional, and let $\alpha = \sup g(C)$ and $\beta = \inf g(C)$. Then*

(i) The sets $E_\alpha = \{x \in C : g(x) = \alpha\}$, $E_\beta = \{x \in C : g(x) = \beta\}$ are non-empty, compact, extreme subsets of C .

(ii) The functional g achieves its maximum and minimum values on C at an extreme point of C , that is, there exist $z_1, z_2 \in \text{ext}(C)$ such that

$$g(z_1) = \sup g(C) \quad \text{and} \quad g(z_2) = \inf g(C).$$

(iii) The sets E_α and E_β admit the following representations:

$$E_\alpha = \overline{\text{co}(\text{ext}(C) \cap E_\alpha)} \quad \text{and} \quad E_\beta = \overline{\text{co}(\text{ext}(C) \cap E_\beta)}.$$

Let us remark that the functional g above has a strict maximum on C if and only if it has a strict maximum on $\text{ext}(C)$, i.e. $E_\alpha = \{z_1\}$ iff $\text{ext}(C) \cap E_\alpha = \{z_1\}$. Indeed, it suffices to notice that if $\text{ext}(C) \cap E_\alpha = \{z_1\}$ then by (iii) one has that $E_\alpha = \overline{\text{co}(\text{ext}(C) \cap E_\alpha)} = \overline{\text{co}(\{z_1\})} = \{z_1\}$.

Finally, let us recall a result coming from the theory of probability, see e.g. [63], namely,

Theorem 2.12 (Helly-Bray). *Let $\{\phi_n : n \geq 1\}$ be a sequence of functions from \mathbb{R} to $[0, d]$, which are non-decreasing and right-continuous. Then there exists a non-decreasing, right-continuous function $\phi : \mathbb{R} \rightarrow [0, d]$, and there exists a subsequence ϕ_{n_k} such that*

$$\lim_n \phi_{n_k}(x) = \phi(x),$$

for all continuity points x of ϕ .

Now we can apply the statements above to the ESS problem described before. Let us consider the locally convex Hausdorff space $X = L_*^1(0, \infty; \mathbb{R})$, i.e. a weighted L^1 Banach space with norm $\|\phi\| = \int_0^\infty |\phi(x)| \Pi_*(x) dx$. The set of possible strategies for a mutant population, i.e. the set of possible probability distribution functions of the (non-negative) random critical age, as a subset of the space L_*^1 , is defined as

$$C_0 := \left\{ \phi \in L_*^1(0, \infty; \mathbb{R}) : \phi(a) \in [0, 1], \text{ non-decreasing, right-continuous, } \lim_{a \rightarrow \infty} \phi(a) = 1 \right\}.$$

Here and below one has to understand that there is a member of the equivalence class which takes values in $[0, 1]$, is non-decreasing, etc. The set C_0 is convex but not compact (e.g. it is not closed), however we can consider a bigger set relaxing the last condition above, namely,

$$C := \left\{ \phi \in L_*^1(0, \infty; \mathbb{R}) : \phi(a) \in [0, 1], \text{ non-decreasing, right-continuous} \right\} \supset C_0. \quad (2.39)$$

With regard to the latter bigger set, we have the following

Proposition 2.13. *The set C defined in (2.39) is a non-empty compact convex subset of the Banach space L_*^1 .*

Proof. The set C is obviously a non-empty subset of L_*^1 , and it is convex since any convex combination $t\phi + (1-t)\psi$, $0 \leq t \leq 1$ and $\phi, \psi \in C$, is a non-decreasing, right-continuous function with values in $[0, 1]$.

The compactness is derived as follows. By the Helly-Bray theorem, see Theorem 2.12, for any sequence of C there exists a subsequence such that converges pointwise to a function of C for all continuity points of the limit function and hence almost everywhere. By the Lebesgue dominated convergence theorem, see e.g. [14], the latter convergence is in L_*^1 sense. Hence, C is a relatively compact set in L_*^1 . The fact that the latter limit function belongs to C implies that the set C is closed (each L_*^1 -convergent sequence of C has a L_*^1 -convergent subsequence with limit in C). Therefore C is a compact set in L_*^1 . \square

Let us recall that for a given $l \geq 0$, the symbol $\mathcal{X}_{[l, \infty)}$ denotes a Heaviside step function, i.e. $\mathcal{X}_{[l, \infty)} : [0, \infty) \rightarrow [0, 1]$, $\mathcal{X}_{[l, \infty)}(a) = 1$ if $a \geq l$ and $\mathcal{X}_{[l, \infty)}(a) = 0$ otherwise. Now, let us consider the following closed (therefore compact) subset of C

$$V := \{\mathcal{X}_{[l, \infty)} : l \geq 0\} \cup \{0\} \subset C \subset L_*^1, \quad (2.40)$$

and we have the following

Proposition 2.14. *The set of the extreme points of C in (2.39), is given by the set V defined in (2.40). In symbols, $\text{ext}(C) = V$.*

Proof. Firstly, let us show that $\text{ext}(C) \subset V$, or equivalently, any function in C which is not in V cannot be an extreme point of C . Indeed, let us take $\phi \in C \setminus V$, hence there exists a point (an age) $\bar{a} \geq 0$ such that $0 < \phi(\bar{a}) < 1$ and let us define

$$\psi_1(a) = \begin{cases} \frac{\phi(a)}{\phi(\bar{a})} & a < \bar{a} \\ 1 & a \geq \bar{a} \end{cases}, \quad \psi_2(a) = \begin{cases} 0 & a < \bar{a} \\ \frac{\phi(a) - \phi(\bar{a})}{1 - \phi(\bar{a})} & a \geq \bar{a} \end{cases}$$

which clearly belong to C and we get for $t = \phi(\bar{a})$, $t\psi_1(a) + (1-t)\psi_2(a) = \phi(a)$, $a \geq 0$, i.e. ϕ is not an extreme point of C . Notice that we have explicitly built a proper convex combination of two functions in C .

Finally, let us show that $V \subset \text{ext}(C)$. Indeed, let us suppose the contrary: $\mathcal{X}_{[l, \infty)}(a)$, $l \geq 0$, is not an extreme point, i.e. it is a proper convex combination of two other functions in C :

$$\mathcal{X}_{[l, \infty)}(a) = t\psi_1(a) + (1-t)\psi_2(a), \quad a \geq 0, \quad \psi_1 \neq \psi_2, \quad 0 < t < 1.$$

On the one hand, if $a < l$, $0 = t\psi_1(a) + (1-t)\psi_2(a)$ then $\psi_1(a) = \psi_2(a) = 0$ for all $a < l$. On the other hand, if $a \geq l$, $1 = t\psi_1(a) + (1-t)\psi_2(a)$ then $\psi_1(a) = \psi_2(a) = 1$ for all $a \geq l$. So, combining both results we have that $\psi_1(a) = \psi_2(a)$, $a \geq 0$, which is a contradiction. \square

Summarizing, the extreme (or extremal) points of C , which is a non-empty compact convex set containing the set of possible strategies C_0 , turn out to be the Heaviside step functions.

Finally, in order to state the main results of the section, let us assume that the female and male fertilities, and the survival probability with the interactions set by the resident population, i.e. $\beta_*(a) = \beta(a, P^*)$ and $\gamma_*(a) = \gamma(a, P^*)$, and $\Pi_*(a) = e^{-\int_0^a \mu(y, P^*) dy}$, are sufficiently smooth with respect to age a .

Now, with the theory developed so far, we are ready to show that an ESS pdf of the random critical age in a sequential hermaphrodite species is a strategy such that all individuals of the population change sex at the same age.

It is worth to mention that next propositions can be considered as a generalization, in the sense that we allow individuals to change sex according to an arbitrary probability distribution function (i.e. the set of feasible strategies is the set of the pdf's), and we have included density-dependent effects in both fertilities and mortality, of the results obtained by E.L. Charnov in [32] chapter 9, and [33] section 2.4. See also [44].

Proposition 2.15 (ESS for the age at sex-reversal). *Let (\hat{l}, P^*) be a positive solution of the following two-dimensional non-linear system*

$$\left\{ \begin{array}{l} \gamma_*(\hat{l}) \int_0^{\hat{l}} \beta_*(x) \Pi_*(x) dx = \beta_*(\hat{l}) \int_{\hat{l}}^{\infty} \gamma_*(x) \Pi_*(x) dx \\ \int_0^{\infty} \Pi_*(x) dx + P^* h \int_{\hat{l}}^{\infty} \Pi_*(x) dx = P^* \int_0^{\hat{l}} \beta_*(x) \Pi_*(x) \int_{\hat{l}}^{\infty} \gamma_*(x) \Pi_*(x) \end{array} \right. , \quad (2.41)$$

fulfilling the inequality $\frac{\beta_*'(\hat{l})}{\beta_*(\hat{l})} < \frac{\gamma_*'(\hat{l})}{\gamma_*(\hat{l})}$ and let us assume that there is no $l \neq \hat{l}$ such that

$$\frac{\beta_*(l)}{\gamma_*(l)} = \frac{\int_0^{\hat{l}} \beta_*(x) \Pi_*(x) dx}{\int_{\hat{l}}^{\infty} \gamma_*(x) \Pi_*(x) dx} . \quad (2.42)$$

Moreover let us assume that (2.27) holds for $u^*(a) = \frac{P^* \Pi_*(a)}{\int_0^{\infty} \Pi_*(x) dx}$, $a \geq 0$.

Then the Heaviside step function $\hat{s}(a) = \mathcal{X}_{[\hat{l}, \infty)}(a)$, $a \geq 0$, is an unbeatable strategy or evolutionarily stable strategy (ESS).

Proof. First notice that the second equation in (2.41), which is equation (2.38) for $\hat{s} = \mathcal{X}_{[\hat{l}, \infty)}$, assures that the system for the resident population adopting strategy \hat{s} has a non-trivial equilibrium and, in addition, the inequality (2.27) guarantees that the latter is locally asymptotically stable.

In view of (2.37) it suffices to show that the continuous affine functional $g : L_*^1 \rightarrow \mathbb{R}$ defined as

$$g(\phi_i) := \frac{\int_0^\infty \beta_*(x) (1 - \phi_i(x)) \Pi_*(x) dx}{\int_0^\infty \beta_*(x) (1 - \hat{s}(x)) \Pi_*(x) dx} + \frac{\int_0^\infty \gamma_*(x) \phi_i(x) \Pi_*(x) dx}{\int_0^\infty \gamma_*(x) \hat{s}(x) \Pi_*(x) dx}, \quad (2.43)$$

has a strict maximum at $\phi_i = \hat{s} \in C_0 \subset C$ when considered on the non-empty compact convex set C defined in (2.39). See Proposition 2.13. By Theorem 2.11, the functional g achieves its maximum value on C at an extreme point of C , i.e. at a point of the set V given by (2.40). See Proposition 2.14. Moreover, as we have seen before, if g has a strict maximum on $\text{ext}(C)$ then it has a strict maximum on C .

Let us consider the function of a real variable $\bar{g} : [0, \infty) \rightarrow \mathbb{R}$ defined as $\bar{g}(l_i) := g(\mathcal{X}_{[l_i, \infty)})$, i.e.,

$$\bar{g}(l_i) := \frac{\int_0^{l_i} \beta_*(x) \Pi_*(x) dx}{\int_0^{l_i} \beta_*(x) \Pi_*(x) dx} + \frac{\int_{l_i}^\infty \gamma_*(x) \Pi_*(x) dx}{\int_{l_i}^\infty \gamma_*(x) \Pi_*(x) dx},$$

which has a strict maximum at \hat{l} if $\bar{g}'(\hat{l}) = 0$, \hat{l} is the unique critical point of \bar{g} , and $\bar{g}''(\hat{l}) < 0$. So, computing the first derivative, we arrive at

$$\bar{g}'(\hat{l}) = \left(\frac{\beta_*(l_i)}{\int_0^{\hat{l}} \beta_*(x) \Pi_*(x) dx} - \frac{\gamma_*(l_i)}{\int_{\hat{l}}^\infty \gamma_*(x) \Pi_*(x) dx} \right) \Pi_*(l_i) \Big|_{l_i=\hat{l}} = 0,$$

by the first equation of (2.41), which has \hat{l} as the only solution by (2.42). On the other hand, computing the second derivative we arrive to the condition

$$\bar{g}''(\hat{l}) = \left(\frac{\beta_*'(\hat{l})}{\int_0^{\hat{l}} \beta_*(x) \Pi_*(x) dx} - \frac{\gamma_*'(\hat{l})}{\int_{\hat{l}}^\infty \gamma_*(x) \Pi_*(x) dx} \right) \Pi_*(\hat{l}) + 0 \cdot \Pi_*'(\hat{l}) < 0,$$

which, using again the first equation in (2.41), is equivalent to $\frac{\beta_*'(\hat{l})}{\beta_*(\hat{l})} < \frac{\gamma_*'(\hat{l})}{\gamma_*(\hat{l})}$. □

Proposition 2.16. *Let $\hat{s} \in C_0$ be a probability distribution function such that there is a locally asymptotically stable non-trivial equilibrium of system (2.5) for $s = \hat{s}$, and let assume that \hat{s} is an ESS. Then there exists $\hat{l} > 0$ such that $\hat{s}(a) = \mathcal{X}_{[\hat{l}, \infty)}(a)$, $a \geq 0$. Furthermore, (\hat{l}, P^*) , where P^* is the total population of the equilibrium, is a solution of (2.41).*

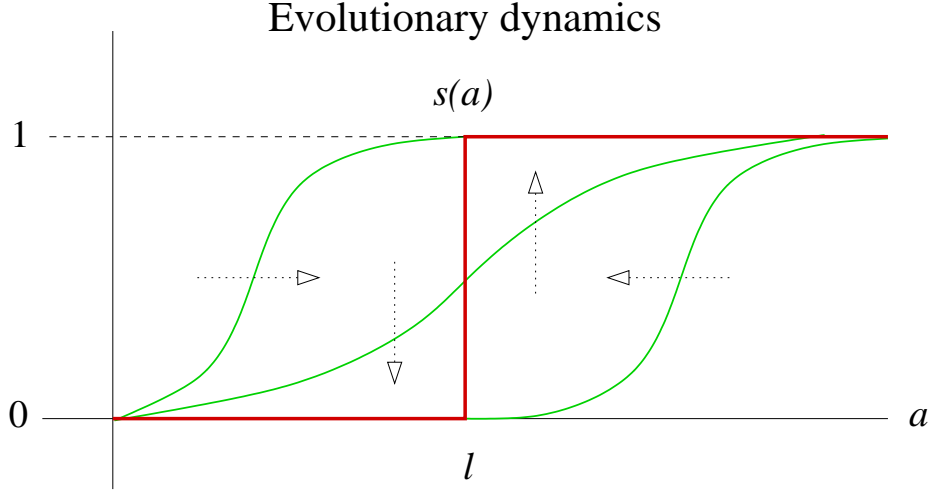


Figure 2.4: ESS (no mutant can invade) for the critical age in a sequential hermaphrodite population: probability distribution function of a measure with the total mass concentrated at a single specific point $a = \hat{l}$, i.e. a Heaviside step function $H(a - \hat{l})$ where the age $\hat{l} > 0$ is the first component of a solution of (2.41).

Proof. By the ESS condition, \hat{s} is a strict maximum of the functional g defined in (2.43) for $\phi_i \in C_0$. We have that g defined on C attains its maximum value in a point $\tilde{s} \in \text{ext}(C) = V$. If $\tilde{s} \neq 0$, it belongs to C_0 and coincides with \hat{s} by hypothesis, and hence \hat{s} is a Heaviside step function. On the other hand, if $\tilde{s} = 0$ then

$$g(\hat{s}) \leq g(\tilde{s}) = \lim_{l \rightarrow \infty} g(\mathcal{X}_{[l, \infty)}) \leq g(\hat{s}) = 2$$

because $\mathcal{X}_{[l, \infty)} \in C_0$ for all $l \geq 0$. So, g attains its maximum value at two points of C , and hence it attains its maximum value at two points of V . That is, $\hat{s} \in V$ i.e. it is a Heaviside step function. \square

In view of (2.41), let us remark that the *adaptive value* of the sex-ratio of a sequential hermaphrodite population at equilibrium, will be ‘in general’ (i.e. when fertilities β and γ are explicitly age-specific) different from one, i.e.

$$\text{sex-ratio} = \frac{\int_0^{\hat{l}} \Pi_*(x) dx}{\int_{\hat{l}}^{\infty} \Pi_*(x) dx} \neq 1.$$

2.9 Sex-ratio

Concerning with the two-dimensional non-linear system of equations (2.41), multiple situations can occur depending on the vital parameters of the population. However, there is an important particular case, namely, when the (density-dependent) fertilities β and γ are age independent. In this case, the adaptive value of the sex-ratio of the population at equilibrium equals to one. The latter is a straightforward consequence of the first equation of (2.41), i.e.

$$\gamma_* \beta_* \int_0^{\hat{l}} \Pi_*(x) dx = \beta_* \gamma_* \int_{\hat{l}}^{\infty} \Pi_*(x) dx .$$

Nevertheless, this case corresponds with an evolutionarily singular strategy with *neutral* evolutionary stability since the strategy $\hat{s}(a) = \mathcal{X}_{[\hat{l}, \infty)}(a)$ is not a strict local maximum of the fitness measure. See e.g. [66].

If in addition, we assume that the (density-dependent) mortality rate is also age independent, namely, $\mu(a, p) := \underline{\mu}(p) \geq \mu_0 > 0$, then we have the following:

$$\frac{\text{age at sex-reversal}}{\text{life expectancy}} = \frac{\hat{l}}{1/\underline{\mu}(P^*)} = \ln 2 \simeq 69.3\% ,$$

which means that, in the case of age-independent vital parameters, individuals change sex when they reach about 69.3% of their expected maximum age.

Indeed, in this case the survival probability is equal to $\Pi_*(a) = e^{-\underline{\mu}(P^*)a}$, and from (2.41) one has that

$$1 = \frac{\int_0^{\hat{l}} \Pi_*(x) dx}{\int_{\hat{l}}^{\infty} \Pi_*(x) dx} = \frac{1 - e^{-\underline{\mu}(P^*)\hat{l}}}{e^{-\underline{\mu}(P^*)\hat{l}}} = e^{\underline{\mu}(P^*)\hat{l}} - 1 ,$$

which implies that $\underline{\mu}(P^*)\hat{l} = \ln 2$.

For empirical data which almost agree with the latter result, see the recent paper [44].

Chapter 3

A model of cyclic parthenogenesis in rotifers

CONTINUING with population dynamics models that takes sexual reproduction into account, in this chapter we are going to study an *haplodiploid* species which exhibits the so-called Cyclic Parthenogenesis (both forms of reproduction: non-sexual and sexual), such as the monogonont rotifers. From the mathematical point of view, here we take the *partial differential equations* approach (see Chapter 1) because we assume that the solution of the problem is sufficiently smooth. Nevertheless, the system that we are going to introduce was originally formulated in a *mild* form of the partial differential equations, see A. Calsina et al. [19] for further details.

We focus on the sexual phase of monogonont rotifers, where the population is made up of three subclasses: virgin and mated mictic females (diploid), and haploid males. The model system has an attractor which can be either an equilibrium solution or a periodic orbit. We will show that the periodic solution appears thanks to a supercritical Hopf bifurcation. So, we present an example of a Hopf bifurcation in a continuously age-structured population model.

3.1 Introduction

Monogonont rotifers are small micro-invertebrate animals who inhabit aquatic media with seasonal variations. These species of rotifers have males, and females which produce two types of eggs. Reproduction in rotifers is of considerable interest because they have a rather complex life history. Their reproductive cycle is the *Cyclic Parthenogenesis*, a combination of sexual and asexual reproduction (two phases).

This cycle begins after the hatching (eclosion) of *resting eggs* (eggs that stay dormant during long periods of time under adverse environmental conditions). These eggs become amictic females (*diploid*: two series of chromosomes). So, in this first asexual phase there is no male presence. There are only amictic females producing diploid eggs that hatch right away to become new amictic females.

The start of the second phase of the reproductive cycle is induced by environmental factors, such as dense population or by deterioration of the environment (see [29], [8] and [7]). In this second phase, there is sexual reproduction and it takes place simultaneously with the other phase.

The amictic females begin to produce amictic daughters and mictic (sexual) ones, these latter at a constant rate B . The virgin mictic daughters produce *haploid* eggs (only one series of chromosomes) which become males after hatching. They can also be fertilized by the males during the first hours of their lives, i.e., before age \tilde{T} , which is called the threshold age of fertilization (see [70]). If the mictic daughters are not fertilized, when they reach maturity at an age M , which is greater or equal than the threshold age of fertilization, they produce eggs that become haploid males. On the other hand, if they have been fertilized, the eggs that they produce are resting eggs (diploid), and then the reproductive cycle begins again. Hence, in optimal environmental conditions, the males do not contribute to the preservation of the species.

The age-structured population dynamics model for the sexual phase of monogonont rotifers presented here, considers the population split into three subclasses: the *virgin mictic females* (male-producing), the *mated mictic females* (resting egg-producing), and the *haploid males*. The diagram in Figure 3.1 shows the reproduction phases of the Cyclic Parthenogenesis exhibited by the species of monogonont rotifers.

The motivations of this study originate from the paper by A. Calsina, J.M. Mazón, and M. Serra [19], and the previous one by E. Aparici et al. [8]. They present numerical evidence that the population of monogonont rotifers is at a stable equilibrium for experimentally obtained values of the parameters (see [8] and [7]) and undertake a study of the *evolutionarily stable value* (ESS, in the sense of [59]) of the threshold age of fertilization. Their result is critically dependent upon the assumption that the demographic equilibrium is prevalent in the mictic phase, requiring a relatively long sexual phase (see [8] p. 655, [30]).

Our contribution to the problem is to prove analytically the stability of this equilibrium for the reference values of the parameters and, however, also to show that the equilibrium can be unstable for values of the parameters not too far from the used ones in [8] and [19]. In case of instability we show analytically that the equilibrium undergoes a supercritical Hopf bifurcation to a (stable) limit cycle. A study of this unstable equilibrium case from the evolutionary point of view seems

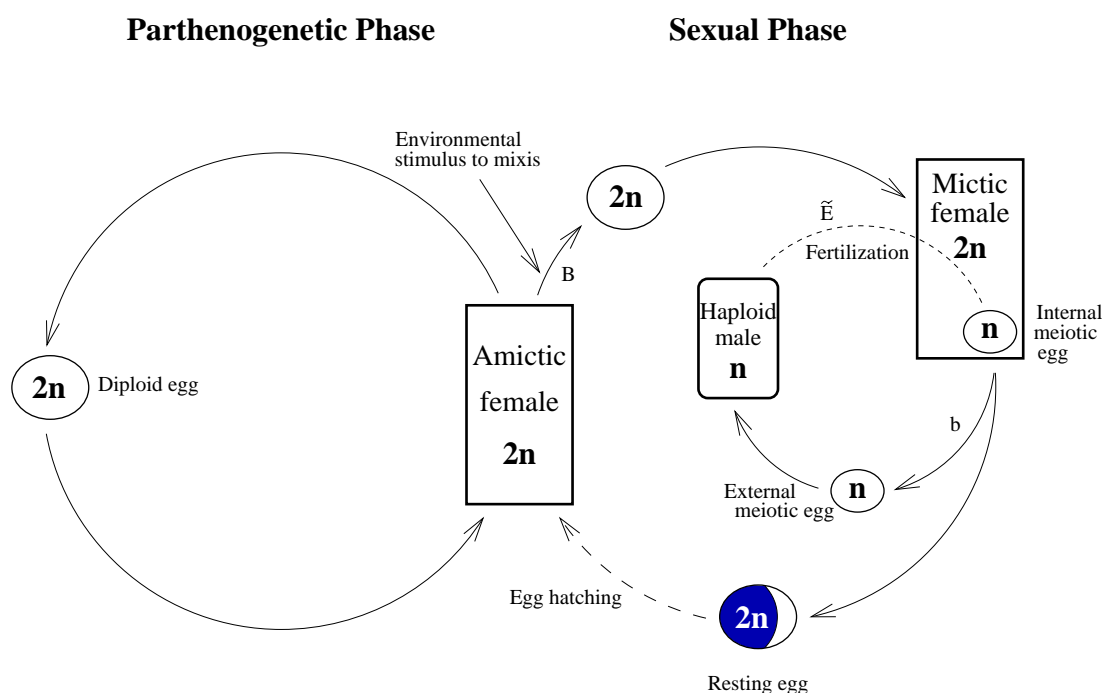


Figure 3.1: Two phases of the reproductive cycle of monogonont rotifers (Cyclic Parthenogenesis [7]). During the sexual phase of this species of rotifers the population is composed of three subclasses: virgin mictic females, mated mictic females, both diploid ($2n$), and haploid males (n). There are two types of eggs: *haploid eggs* produced by virgin females, and *resting eggs* produced by mated ones.

attainable, at least numerically. Several authors have already considered evolutionarily stable strategies in the case of ecological systems with non-trivial attractors (see for instance [65]).

In [12] a Hopf bifurcation theorem for a non-linear age dependent population dynamics problem with density dependence on some “measure” of the population is proved using the method of (Z)- A spaces of Desch and Schappacher. In [43] the authors documented a Hopf bifurcation in an actual rotifer-algal chemostat system with two age classes for the rotifer population. Nonetheless, their model is focused on the asexual reproduction phase. For other examples of Hopf bifurcations in structured population dynamics see the recent works [21], [50].

3.2 Formulation of the model

First of all we introduce some terminology according to [19]. Afterwards, we state the problem using a simplified (in variables and parameters) system.

Let $\alpha, \tau \in [0, \infty)$ be age and time respectively.

The state variables are: $\tilde{v}(\alpha, \tau)$ the density with respect to age of virgin mictic females at time τ , $m(\alpha, \tau)$ the density with respect to age of mated mictic females at time τ , and $\tilde{h}(\alpha, \tau)$ the density with respect to age of haploid males at time τ , which we think as non-negative functions. The total population of each subclass is computed by integrating over the age span. So, the total population at time τ of virgin mictic females and mated mictic females are $\tilde{V}(\tau) = \int_0^\infty \tilde{v}(x, \tau) dx$ and $\int_0^\infty m(x, \tau) dx$, respectively, and the total population of haploid males at time τ is $\tilde{H}(\tau) = \int_0^\infty \tilde{h}(x, \tau) dx$.

So, we are in the functional framework of $L^1 := L^1(0, \infty; \mathbb{R})$, the Banach space of equivalence classes of Lebesgue integrable functions from $[0, \infty)$ to \mathbb{R} which agree almost everywhere (a.e.), equipped with the norm $\|\phi\|_{L^1} := \int_0^\infty |\phi(x)| dx$.

The parameters of the model are shown in Table 3.1.

These parameters are assumed to be time-independent and to satisfy: $\tilde{\mu}, \tilde{\delta}, \tilde{E}, B, b > 0$ and $0 < \tilde{T} \leq M$. For further convenience we remark that the reference values of these parameters are $\tilde{\mu} = 0.4 \text{ day}^{-1}$, $\tilde{\delta} = 0.7 \text{ day}^{-1}$, $\tilde{E} = 0.04 \text{ male}^{-1} \text{ day}^{-1}$, $B = 24 \text{ females day}^{-1}$, $b = 1.5 \text{ males female}^{-1} \text{ day}^{-1}$, $M = 1 \text{ day}$, and \tilde{T} between 0.3 and 0.5 days (see [8]).

The population densities satisfy the following system of non-linear partial integro-differential equations,

$$\begin{cases} \frac{\partial}{\partial \tau} \tilde{v}(\alpha, \tau) + \frac{\partial}{\partial \alpha} \tilde{v}(\alpha, \tau) + \tilde{\mu} \tilde{v}(\alpha, \tau) &= -\tilde{E} \tilde{H}(\tau) \tilde{v}(\alpha, \tau) \mathcal{X}_{[0, \tilde{T}]}(\alpha) \\ \frac{\partial}{\partial \tau} m(\alpha, \tau) + \frac{\partial}{\partial \alpha} m(\alpha, \tau) + \tilde{\mu} m(\alpha, \tau) &= \tilde{E} \tilde{H}(\tau) \tilde{v}(\alpha, \tau) \mathcal{X}_{[0, \tilde{T}]}(\alpha) \\ \frac{\partial}{\partial \tau} \tilde{h}(\alpha, \tau) + \frac{\partial}{\partial \alpha} \tilde{h}(\alpha, \tau) + \tilde{\delta} \tilde{h}(\alpha, \tau) &= 0 \end{cases} \quad (3.1)$$

and boundary conditions $\tilde{v}(0, \tau) = B$, $m(0, \tau) = 0$, $\tilde{h}(0, \tau) = b \int_M^\infty \tilde{v}(x, \tau) dx$.

These type of systems are sometimes referred in the literature as nonlocal non-linear first-order hyperbolic partial differential equations.

The equations are based on the *Balance law* of the population, with constant mortality rates $(\tilde{\mu}, \tilde{\delta})$ and with a non-linear term modelling the change of mictic females from virgin to mated. The right hand side of the first equation in (3.1) means that the haploid males fertilize the virgin mictic females while they are under \tilde{T} age. We recall that $\mathcal{X}_{[0, \tilde{T}]}(\alpha)$ is the characteristic function,

$\tilde{\mu}$	the per capita death rate for females
$\tilde{\delta}$	the per capita death rate for males
\tilde{E}	the male-female encounter rate
B	the recruitment rate of mictic females
b	the fertility of male-producing mictic females
M	the age at maturity for females
\tilde{T}	the threshold age of fertilization

Table 3.1: Parameters of the model for the phase of sexual reproduction in monogonont rotifers.

namely, its value is 1 if $\alpha \in [0, \tilde{T}]$ and 0 otherwise.

The *Birth law*, that is to say, the input of population of age 0 has an age-specific fertility modulus of the form $b \mathcal{X}_{[M, \infty)}(x)$, for haploid males. In the case of virgin mictic females, we can assume that the birth function is a constant B (see [8]), and of course, there are no mated mictic females of age 0, thus giving a zero input of the mated ones.

We want to point out that system (3.1) shows, on the one hand, features of an asexual reproduction model like the constant influx of virgin mictic females and the fact that the influx of haploid males is proportional to the mature virgin mictic females. On the other hand, it also shows features of a sexual reproduction model like the *transition* from virgin to mated. Moreover, notice that the per capita transition rate is density-dependent, i.e. $\tilde{E} \tilde{H}(\tau) \mathcal{X}_{[0, \tilde{T}]}(\alpha)$. So, roughly speaking, it could be said that the system is ‘affine’ due to the parthenogenetic phase, and it is non-linear due to the sexual phase.

For a monograph on the subject of age-dependent population dynamics see, for instance, the book by G.F. Webb [74] or the book by M. Iannelli [53].

In [19], the authors prove the existence and uniqueness of non-negative *mild* solutions to system (3.1) with initial conditions in L^1_+ , the non-negative cone in L^1 , which are defined for all $\tau \geq 0$.

The equation of mated mictic females, second equation in (3.1), is uncoupled from the others, and we consider it separately. If we know the population of virgin females and haploid males, we will easily find the population of mated ones. Indeed, adding the first and second equations in (3.1) we get a linear first-order hyperbolic partial differential equation, which can be integrated explicitly by the method of characteristic curves.

3.2.1 Nondimensionalized system

We introduce a rescaling in order to reduce the number of parameters. This change only affects the units of age, time, and population:

$$\begin{aligned} \alpha &= M a & \tau &= M t \\ \tilde{v}(\alpha, \tau) &= B v(a, t) & \tilde{h}(\alpha, \tau) &= B b M h(a, t). \end{aligned}$$

Introducing four new (nondimensional) parameters related to the seven old ones according to: $\mu = \tilde{\mu} M$, $\delta = \tilde{\delta} M$, $E = \tilde{E} B b M^3$, $T = \frac{\tilde{T}}{M}$, the system of equations to be satisfied by the new population densities (only virgin mictic females and haploid males) becomes:

$$\begin{cases} \frac{\partial}{\partial t} v(a, t) + \frac{\partial}{\partial a} v(a, t) + \mu v(a, t) = -E H(t) v(a, t) \mathcal{X}_{[0, T]}(a) \\ \frac{\partial}{\partial t} h(a, t) + \frac{\partial}{\partial a} h(a, t) + \delta h(a, t) = 0 \end{cases} \quad (3.2)$$

with boundary conditions

$$v(0, t) = 1 \quad , \quad h(0, t) = \int_1^{\infty} v(x, t) dx, \quad (3.3)$$

where a is the age, t is the time (with the new units) and the parameters are: $\mu, \delta, E > 0$ and $0 < T \leq 1$. Now, the age at maturity for females is 1. We also recall that the total population of haploid males at time t is $H(t) = \int_0^{\infty} h(x, t) dx$.

From now on, we adopt the notation $\dot{\cdot} \equiv \frac{\partial}{\partial t}$, $' \equiv \frac{\partial}{\partial a}$, and $\mathcal{X} \equiv \mathcal{X}_{[0, T]}$.

3.3 Equilibrium solution

We look for an equilibrium solution of (3.2) and (3.3): a solution in the sense of Webb [74] ($v^*(a), h^*(a)$) independent of time, that is they belong to the Sobolev space $W^{1,1}(0, \infty)$ (see e.g. [14]). In particular, this implies that $v^*(a)$ and $h^*(a)$ are absolutely continuous functions.

This is done by solving the initial value problem: $v' + \mu v = -E H v \mathcal{X}$, $h' + \delta h = 0$, with “initial conditions” $v(0) = 1$ and $h(0) = \int_1^{\infty} v(x) dx$, and with $H = \int_0^{\infty} h(x) dx$. Calling H^* the males population at equilibrium, the first differential equation plus its boundary condition, plus continuity, imply

$$v^*(a) = \begin{cases} e^{-(\mu + E H^*) a} & a \in [0, T] \\ e^{-(\mu a + E H^* T)} & a \in [T, \infty) \end{cases}$$

This gives a total population of virgin females equal to

$$V^* = \frac{\mu + E H^* e^{-(\mu + E H^*) T}}{\mu(\mu + E H^*)}.$$

The second differential equation gives $h^*(a) = \delta H^* e^{-\delta a}$, and its boundary condition combined with the formula for $v^*(a)$ imply that H^* solves the transcendental equation:

$$\mu \delta H^* = e^{-(\mu + E H^* T)} \quad (3.4)$$

For any positive values of μ, δ, E and T , (3.4) has a unique solution that belongs to the interval $(0, \frac{e^{-\mu}}{\mu \delta})$. Consequently, there is a unique stationary solution of (3.2) and (3.3) which is given above, with H^* (the total population of haploid males) being the solution of (3.4).

3.4 Linear stability analysis

In this section we linearize system (3.2) and (3.3) in a neighbourhood of the equilibrium point (see Section 3.4.2 for a proof of the principle of linearized stability). The first step is to shift the equilibrium to the origin. For convenience we use the same names for the new variables,

$$\overbrace{v(a, t)}^{\text{old}} = v^*(a) + \overbrace{v(a, t)}^{\text{new}} \quad , \quad \overbrace{h(a, t)}^{\text{old}} = h^*(a) + \overbrace{h(a, t)}^{\text{new}} .$$

So,

$$\begin{cases} \dot{v} + v' + \mu v = -E((H^* + H)v + H v^*) \mathcal{X} \\ \dot{h} + h' + \delta h = 0 \end{cases} \quad (3.5)$$

$$v(0, t) = 0 \quad , \quad h(0, t) = \int_1^\infty v(x, t) dx =: V_1(t)$$

The integrable continuous solutions with separate variables of the linearized system (obtained by dropping $-E H v \mathcal{X}$ in (3.5)) are $v = e^{\lambda t} u_1(a)$ and $h = e^{\lambda t} u_3(a)$, where $\lambda \in \mathbb{C}$ (the eigenvalues) is a constant, and

$$u_1(a) = c \begin{cases} \frac{E e^{(\lambda + \mu)(T-1)}}{\lambda(\lambda + \mu)(\lambda + \delta)} e^{-(\mu + E H^*)a} (e^{-\lambda a} - 1) & a \in [0, T] \\ e^{(\lambda + \mu)(T-a)} & a \in [T, \infty) , \end{cases}$$

$$u_3(a) = c \frac{e^{(\lambda + \mu)(T-1)}}{\lambda + \mu} e^{-(\lambda + \delta)a} , \quad c \in \mathbb{C} \text{ an arbitrary constant ,}$$

with an additional condition, namely, $\text{Re}(\lambda) > -\mu, -\delta$, and $\lambda \neq 0$ (a direct computation shows that $\lambda = 0$ is never an eigenvalue). Since continuity at $a = T$ (the threshold age of fertilization) must hold, λ must satisfy the so-called *Characteristic equation*

$$\lambda(\lambda + \mu)(\lambda + \delta) = E \mu \delta H^* (e^{-\lambda} - e^{(T-1)\lambda}) . \quad (3.6)$$

Before undertaking a study of the equation (3.6), let us use it to write the solution of the linearized system (the eigenfunction) as follows

Population density	Total population
$u_1(a) = c \begin{cases} \frac{v^*(a)(e^{-\lambda a}-1)}{v^*(T)(e^{-\lambda T}-1)} & a \in [0, T] \\ e^{(\lambda+\mu)(T-a)} & a \in [T, \infty) \end{cases}$	$U_1 = c \frac{\frac{v^*(T)-1}{\mu+EH^*} + \frac{1-v^*(T)e^{-\lambda T}}{\lambda+\mu+EH^*}}{v^*(T)(e^{-\lambda T}-1)} + \frac{c}{\lambda+\mu}$
$u_3(a) = c \frac{e^{(\lambda+\mu)(T-1)}}{\lambda+\mu} e^{-(\lambda+\delta)a}$	$U_3 = c \frac{\lambda}{E v^*(T)(e^{-\lambda T}-1)}$

This form of the eigenfunction will be used in Section 3.5.1. In particular, the indices 1 and 3 are taken to agree with the notation of that section.

3.4.1 Characteristic equation

There is no nonvanishing real solution to the *characteristic equation* (3.6) larger than $-\min\{\mu, \delta\}$. Indeed, the *cubic polynomial* on the left hand side and the *linear combination of exponential functions* on the right hand side have opposite sign whenever $\lambda > -\min\{\mu, \delta\}$ and $\lambda \neq 0$.

In order to find complex solutions, we start by solving the case $E = 0$ that has only three roots $\lambda = 0, -\mu, -\delta$ which are unacceptable due to the additional condition. Now we fix the parameters μ, δ, T , and follow these initial roots by analytical continuation of the solutions of (3.6) while varying E . Increasing the parameter E we find valid complex solutions, which finally cross the imaginary axis for the value $E = E_{un}$ as we show next. The equilibrium point remains asymptotically stable until this happens. For a detailed analysis of analogous situations see, for instance, [57] Chap. 5 and [38] Chap. XI.

The purely imaginary solutions $\lambda = \pm\omega i$, $\omega > 0$ are obtained from (3.6) as follows,

$$\omega i(\omega i + \mu)(\omega i + \delta) = E\mu\delta H^* \left(e^{-\omega i} - e^{(T-1)\omega i} \right),$$

$$-(\mu + \delta)\omega^2 + \omega(\mu\delta - \omega^2)i = -2E\mu\delta H^* \sin\left(\omega\frac{T}{2}\right) \left(\sin\left(\omega\left(1 - \frac{T}{2}\right)\right) + i \cos\left(\omega\left(1 - \frac{T}{2}\right)\right) \right), \quad (3.7)$$

and dividing the imaginary part by the real one,

$$\frac{\omega^2 - \mu\delta}{(\mu + \delta)\omega} = \cot\left(\omega\left(1 - \frac{T}{2}\right)\right). \quad (3.8)$$

The important fact about the previous equation is that the parameter E does not appear in it. Hence, once we have the value of ω (the smallest positive solution of (3.8), which lies between

$\sqrt{\mu\delta}$ and $\frac{\pi}{2-T}$), we can find the corresponding value of the parameter E taking the modulus of both sides of (3.7) and using (3.4):

$$E_{un} = K e^{\mu + \frac{TK}{\mu\delta}}, \quad \text{with} \quad K = \frac{\omega \sqrt{(\omega^2 + \mu^2)(\omega^2 + \delta^2)}}{2 |\sin(\omega \frac{T}{2})|}. \quad (3.9)$$

Even though E_{un} is an increasing function of K , the same is not true for K as a function of ω when $\omega > \frac{2\pi}{T}$. So, it is not completely clear that, for fixed values of μ, δ and $0 < T \leq 1$, the smallest solution of (3.8) gives the smallest value of $E_{un} = K e^{\mu + \frac{TK}{\mu\delta}}$ (the actual instability threshold value of the remaining parameter E). Nevertheless, for $\omega > \frac{2\pi}{T}$, we have $K > 4\pi^3$ and $\mu + \frac{TK}{\mu\delta} > \mu + \pi \sqrt{1 + (\frac{\omega}{\mu})^2} > 9.8485$ (the latter follows from a trivial analysis of the function $f(\mu) = \mu + \pi \sqrt{1 + (\frac{2\pi}{\mu})^2}$). Hence, for any $\omega > \frac{2\pi}{T}$, $E_{un} > 2.34 \times 10^6$, which is very far away from the values of the parameter we are interested in (see below).

Consequently, if an instability arises for a set of parameter values μ, δ, T and E_{un} , such that E_{un} is not extremely large, this necessarily corresponds to the first solution of equation (3.8) and, moreover, the relationship between these parameters is given by (3.9), with ω being the smallest positive solution of (3.8). In the four dimensional parameter space (μ, δ, T, E) , the three dimensional stability boundary is the set given by the equation $E = E_{un}(\mu, \delta, T)$ defined in (3.9).

On the other hand, as E_{un} is a strictly increasing function of ω for $\omega < \frac{2\pi}{T}$, the characteristic equation cannot have more than one conjugate pair of purely imaginary solutions for a given choice of the parameter values μ, δ, T and E whenever E is not very large, larger than 2.34×10^6 , say.

For practical purposes, the reference values using the new units are: $\mu = 0.4$, $\delta = 0.7$, and $T = 0.3$. In this case, the smallest positive solution of (3.8) is $\omega = 1.087500525$ (the computation is done by Newton method using the midpoint $\frac{1}{2}(\sqrt{\mu\delta} + \frac{\pi}{2-T})$ as the initial guess) and the instability threshold value $E_{un} = 1617.928392$ is far from the reference value $E = 0.04 \times 24 \times 1.5 \times 1^3 = 1.44$.

Notice that, since E_{un} depends on μ, δ, T , we can take the values $\mu = 0.9355$, $\delta = 1.4463$, and $T = 0.4274$ that minimize the instability threshold value of the encounter rate: $E_{un} = 501.8318829$ (corresponding to $\omega = 1.604377334$).

The pictures in Figure 3.2 show different level surfaces of the scalar-valued function E_{un} of the three independent variables μ, δ, T .

Summarizing, fixing the mortality rates μ, δ and the threshold age of fertilization T , and using the linear stability analysis, we have found that the stationary population is asymptotically stable for values of E (the remaining parameter related to male-female encounter rate) under E_{un} (in particular, for the reference values used in [19]). For E values above this critical value, the

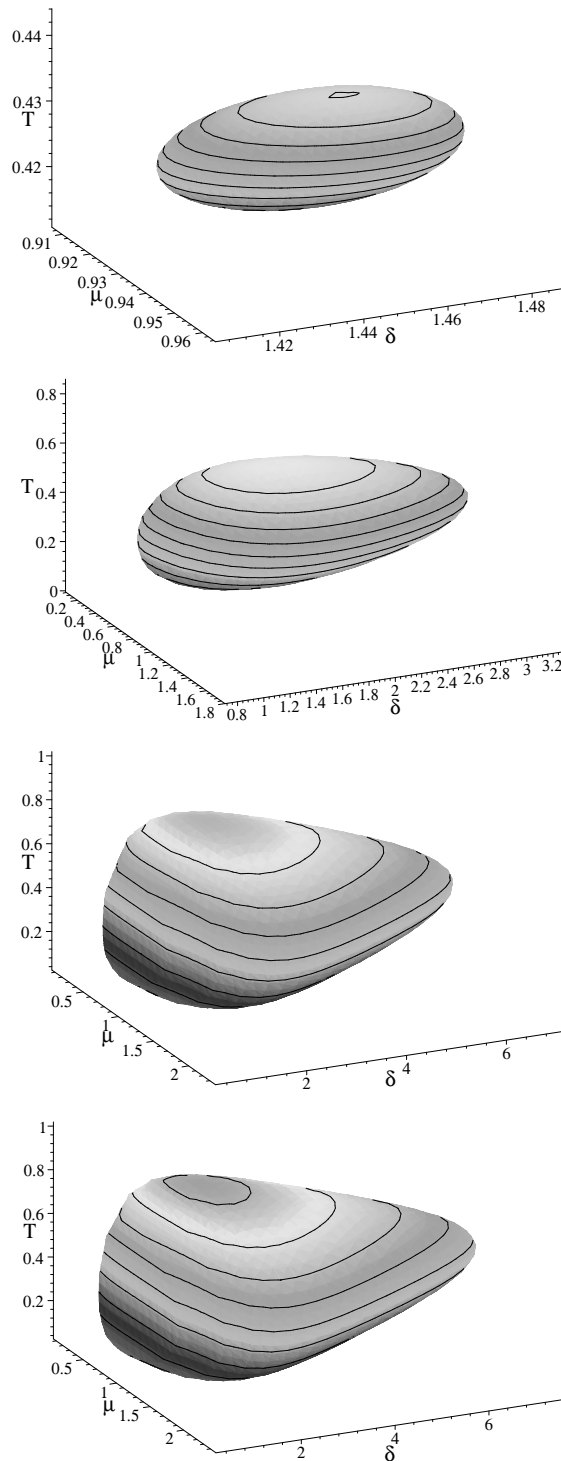


Figure 3.2: Level surfaces of the critical value $E_{un}(\mu, \delta, T)$ regarded as a function of three variables: the mortality rates μ and δ , and the threshold age of fertilization T . From top to bottom, $E_{un} = 502, 680, 1400, 1618$, respectively.

stationary population is unstable. Equivalently, for a given value E_0 of the encounter rate, the points in the (μ, δ, T) space interior to the level surface $E_{un}(\mu, \delta, T) = E_0$ correspond to unstable equilibria.

3.4.2 Principle of linearized stability

The validity of a *strong* principle of linearized stability for system (3.5), in the sense that the origin is (locally) asymptotically stable if the real part of each eigenvalue of the linear part is negative, follows from three different facts.

First, system (3.5) has a standard formulation in L^1 and consequently, a variation of constants equation can be written for it (see [74]), in such a way that the stability of the origin of system (3.5) follows if the solutions of the linearized system (obtained by dropping $-EHv\mathcal{X}$ in (3.5)) tend exponentially to 0, i.e., if the growth bound ω of the linear semigroup $S(t)$ generated by it is negative.

On the other hand, $\omega = \max(\omega_{\text{ess}}, s(A))$, where the *essential growth bound* ω_{ess} of $S(t)$ is defined by

$$\omega_{\text{ess}} = \lim_{t \rightarrow \infty} \frac{\log \|S(t)\|_{\text{ess}}}{t},$$

with $\|S\|_{\text{ess}} := \inf\{\|S - \mathcal{K}\| : \mathcal{K} \text{ is a compact operator}\}$, whereas $s(A)$ stands for the so-called *spectral bound*, i.e. the supremum of the real parts of the spectrum of the infinitesimal generator A (see [62] and [74]). As usual in age-dependent population dynamics (see [74], where a general theorem is stated, not applicable in our case because of lack of smoothness), ω_{ess} turns out to be negative because $S(t)$ can be decomposed, for $t > 1$, as an addition of a compact operator $\mathcal{X}_{[0,t]}(a)S(t)$ plus an exponentially small one, $\mathcal{X}_{(t,\infty)}(a)S(t)$. Indeed, integrating along characteristics one readily obtains that the norm of the second one is less than or equal to $Ce^{-\min\{\mu,\delta\}t}$, for some constant C .

The compactness property of the first one can be shown as follows. Notice that the solution (computed at the beginning of Section 3.4) of the linearized system $(v(a, t), h(a, t))$ for $a < t$ and $t > 1$ can be obtained as the image of the pair $(V_1(\cdot), H(\cdot))$ by a bounded linear operator from the space of (pairs) of continuous functions on $[0, t]$ to $(L^1(0, t))^2$. This bounded linear operator can be explicitly written by the method of characteristics.

Moreover, $(V_1(\cdot), H(\cdot))$ is the unique solution of a system of linear integral equations of the form $(V_1, H) = \mathcal{B}(V_1, H) + \mathcal{K}(v_0, h_0)$, where \mathcal{B} is a bounded linear operator in the space of pairs of continuous functions on $[0, t]$ whereas \mathcal{K} is a compact linear operator (more precisely, a finite rank linear operator) from the space of initial conditions $(L^1(0, \infty))^2$ to the space of

continuous functions. Since the composition of bounded and compact linear operators is compact, the statement follows.

Alternatively, we could have used the somehow reduced formulation (3.11) of Section 3.5.1 to deal with an eventually compact semigroup (i.e. a semigroup which is compact for sufficiently large t) in order to have $\omega_{\text{ess}} = 0$ and to obtain the same conclusions.

Finally, a computation like the previous one in Section 3.4 yielding the eigenvalues and the eigenfunctions, shows that any complex number with real part larger than $-\min\{\mu, \delta\}$ and not satisfying the characteristic equation (3.6) belongs to the resolvent set.

3.5 Hopf bifurcation

Finally we check the hypotheses of the Hopf bifurcation theorem (see [38]). Indeed, there is an equilibrium at the origin, and the linear part of the system (3.5) has a conjugate pair of eigenvalues on the imaginary axis ($\pm\omega i$) at $E = E_{un}$. What we have done until now (in Section 3.4) shows that they are geometrically simple (i.e. $\dim(\ker(A - \omega i I)) = 1$, where A stands for the linear part of the system) and that no other eigenvalue belongs to $\mathbb{Z}\omega i$ (in fact, there are no more purely imaginary eigenvalues at $E = E_{un}$). In Section 3.5.1 we show that the eigenvalues are actually algebraically simple. So, to show the existence of the Hopf bifurcation we just have to compute the real part of the derivative of the critical eigenvalue at the critical value of the parameter $E = E_{un}$. Differentiating (3.6) with respect to E , using (3.4) we get

$$\frac{\partial \lambda}{\partial E} = \frac{1}{E(1 + EH^*T)} \left(\frac{1}{\lambda} + \frac{1}{\lambda + \mu} + \frac{1}{\lambda + \delta} + 1 + \frac{T}{e^{-\lambda T} - 1} \right)^{-1}, \quad (3.10)$$

$$\operatorname{Re} \left(\frac{\partial \lambda}{\partial E}(E_{un}) \right) = \frac{\frac{1}{E_{un}(1 + E_{un}H_{un}^*T)} \left(\frac{\mu}{\omega^2 + \mu^2} + \frac{\delta}{\omega^2 + \delta^2} + 1 - \frac{T}{2} \right)}{\left(\frac{\mu}{\omega^2 + \mu^2} + \frac{\delta}{\omega^2 + \delta^2} + 1 - \frac{T}{2} \right)^2 + \left(\frac{1}{\omega} + \frac{\omega}{\omega^2 + \mu^2} + \frac{\omega}{\omega^2 + \delta^2} - \frac{T}{2} \cot(\omega \frac{T}{2}) \right)^2} > 0,$$

with H_{un}^* the solution of (3.4) at $E = E_{un}$. Since $0 < T \leq 1$, the condition above assures that the eigenvalues cross the imaginary axis with positive speed, and so the existence of a Hopf bifurcation.

Moreover, we have computed the direction of the Hopf bifurcation (see next section for further details). The conclusion is that for the reference values of (μ, δ, T) , the first Lyapunov coefficient is negative, and so, the bifurcation is *supercritical*, i.e., the stable limit cycle exists for values of E larger than the critical value E_{un} .

3.5.1 Direction of the bifurcation

In this section we compute the coefficient E_2 in the expansion $E(\epsilon) = E_{un} + E_2\epsilon^2 + o(\epsilon^2)$ which determines the existence of the limit cycle before or after the parameter E crosses the critical value E_{un} . These two types of bifurcation are called *subcritical* and *supercritical* respectively. Notice that the first Lyapunov coefficient a_1 for the system written in normal form (see e.g. [47]) will have the same sign as $-E_2 \operatorname{Re}(\frac{\partial \lambda}{\partial E}(E_{un}))$, (see [38]). If $E_2 < 0$ the limit cycle is unstable, and if $E_2 > 0$ it is asymptotically stable.

We make another change of state variables that avoids dealing with a non-compact interval for the age and simplifies the boundary conditions. In particular this implies that the problem will be in the sun-reflexive framework (see [38]). We integrate with respect to the age the densities of *mature virgin mictic females* and of *haploid males* in (3.5). Keeping the density of virgin mictic females when they are under maturity age as dependent variable, we get the system (3.11) with three new variables:

$$v(a, t) \Big|_{0 \leq a \leq 1}, \quad V_1(t) = \int_1^\infty v(x, t) dx, \quad H(t) = \int_0^\infty h(x, t) dx.$$

So,

$$\begin{cases} \dot{v} + v' + \mu v &= -E((H^* + H)v + Hv^*)\mathcal{X} \\ \dot{V}_1 - v(1, t) &= -\mu V_1 \\ \dot{H} - V_1 &= -\delta H \end{cases} \quad (3.11)$$

$$v(0, t) = 0, \quad \text{age } a \in [0, 1]$$

Notice that we have reduced the system in the sense that now there are no nonlocal terms and the age span is bounded.

We split system (3.11) into a linear operator A (with a conjugate pair of purely imaginary eigenvalues) plus a remaining non-linear part R :

$$\begin{pmatrix} \dot{v} \\ \dot{V}_1 \\ \dot{H} \end{pmatrix} = \begin{pmatrix} -\frac{\partial}{\partial a} - \mu - E_{un}H_{un}^*\mathcal{X} & 0 & -E_{un}v_{un}^*(a)\mathcal{X} \\ \operatorname{eval}(\cdot, 1) & -\mu & 0 \\ 0 & 1 & -\delta \end{pmatrix} \begin{pmatrix} v \\ V_1 \\ H \end{pmatrix} + R \begin{pmatrix} v \\ V_1 \\ H \end{pmatrix},$$

$$R \begin{pmatrix} v \\ V_1 \\ H \end{pmatrix} = ((E_{un}H_{un}^* - EH^*)v + (E_{un}v_{un}^*(a) - Ev^*(a))H - EHv)\mathcal{X} \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}.$$

Let us remark that we have rewritten the system as an non-linear evolution equation in a certain Banach space.

The first step to compute the coefficient E_2 in the expansion of $E(\epsilon)$, is to find the eigenvectors of the operator A , defined in $X = L^1(0, 1) \times \mathbb{C}^2$, with domain the elements $u = (u_1(a), U_2, U_3)$ of X which first component is an absolutely continuous function vanishing at 0, and also of the operator A^* , the adjoint operator of A , defined in $X^* = L^\infty(0, 1) \times \mathbb{C}^2$ with domain the vectors $\varphi = (\varphi_1(a), \Phi_2, \Phi_3)$ of X^* which first component is a Lipschitz function such that $\varphi_1(1) = \Phi_2$. The adjoint operator is

$$A^* = \begin{pmatrix} \frac{\partial}{\partial a} - \mu - E_{un}H_{un}^*\mathcal{X} & 0 & 0 \\ 0 & -\mu & 1 \\ -E_{un} \int_0^T v_{un}^*(x) \cdot dx & 0 & -\delta \end{pmatrix}$$

According to [38], we take the following duality pairing:

$$\langle \varphi, u \rangle = \int_0^1 \varphi_1(x) u_1(x) dx + \Phi_2 U_2 + \Phi_3 U_3.$$

Let u and φ be the eigenvectors at $\lambda = \omega i$ of A and A^* respectively:

$$\begin{aligned} u_1(a) &= c \begin{cases} e^{c_0(T-a)} \frac{e^{-\omega i a} - 1}{e^{-\omega i T} - 1} & a \in [0, T] \\ e^{c_1(T-a)} & a \in [T, 1] \end{cases} & \varphi_1(a) &= c^* \begin{cases} e^{(c_0 + \omega i)(a-T)} & a \in [0, T] \\ e^{c_1(a-T)} & a \in [T, 1] \end{cases} \\ U_2 &= c \frac{e^{c_1(T-1)}}{c_1} & \Phi_2 &= c^* e^{c_1(1-T)} \\ U_3 &= c \frac{\omega i e^{c_0 T}}{E_{un}(e^{-\omega i T} - 1)} & \Phi_3 &= c^* c_1 e^{c_1(1-T)} \end{aligned}$$

with $c_0 = \mu + E_{un}H_{un}^* \in \mathbb{R}$, $c_1 = \omega i + \mu$, and c, c^* nonvanishing complex arbitrary numbers. As $\langle \varphi, u \rangle = c^* c (E_{un}(1 + E_{un}H_{un}^* T) \frac{\partial \lambda}{\partial E}(E_{un}))^{-1} \neq 0$ using (3.10), the eigenvalues are algebraically simple and we can normalize to $\langle \varphi, u \rangle = 1$ taking c^*, c such that their product equals

$$E_{un}(1 + E_{un}H_{un}^* T) \frac{\partial \lambda}{\partial E}(E_{un}).$$

By **Theorems X.2.6** and **X.3.7** in [38] chapter X, Diekmann et al., there exist even functions $E(\epsilon) = E_{un} + E_2 \epsilon^2 + o(\epsilon^2)$ and $\omega(\epsilon) = \omega + o(\epsilon)$ defined for ϵ sufficiently small such that system (3.11) for $E = E(\epsilon)$ has a $\frac{2\pi}{\omega(\epsilon)}$ -periodic orbit of radius $\mathcal{O}(\epsilon)$. Using the explicit formula in the Theorem 3.7 in [38] we compute the third term E_2 in the Taylor expansion of E . Since the third derivative of R vanishes identically and R maps X into $X \subset X^{\odot*}$ (see [38]), this coefficient reduces to

$$E_2 = - \frac{\operatorname{Re} (\langle \varphi, D_1^2 R_{un}(-A^{-1} D_1^2 R_{un}(u, \bar{u}), u) \rangle + \frac{1}{2} \langle \varphi, D_1^2 R_{un}((2\omega i - A)^{-1} D_1^2 R_{un}(u, u), \bar{u}) \rangle)}{\operatorname{Re} \left(\frac{\partial \lambda}{\partial E}(E_{un}) \right)},$$

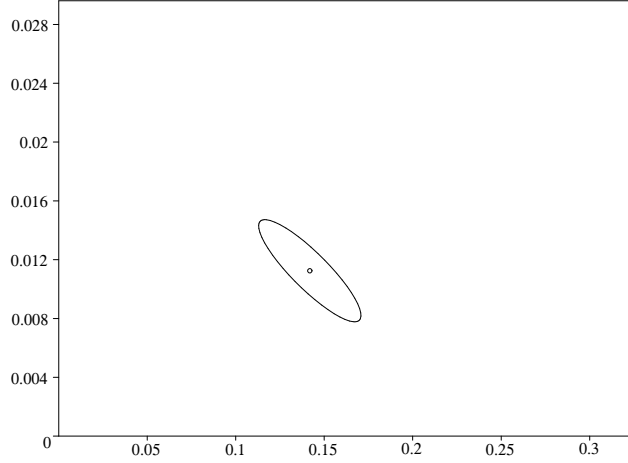


Figure 3.3: Total populations (females vs. males) of a *first approximation* of the limit cycle around its equilibrium, i.e. $(V^*, H^*) + \text{Re}(e^{\omega it}(U_1, U_3))$ with $c = \sqrt{\frac{E - E_{un}}{E_2}}$ and $E_2 = 482005 > 0$ (see Sections 3.4 and 3.5.1), for $\mu = 0.9355$, $\delta = 1.4463$, $T = 0.4274$ and $E = 675.84 > E_{un}$. The equilibrium is unstable: $\text{Re}(\lambda) = 0.0387 > 0$, and the periodic orbit is stable, arising from a supercritical Hopf bifurcation.

where $D_1^2 R_{un} = D_1^2 R(0, E_{un})$ is the second derivative of the non-linear part of the system at the origin for the critical value of the parameter E , and the bar stands for complex conjugation. Notice that the resolvent operator of A can be explicitly computed solving an inhomogeneous linear first-order ordinary differential equation with piecewise constant coefficients. After several simplifications, we get the following explicit formula:

$$E_2 = \frac{|c|^2 E_{un} e^{2c_0 T}}{2} \left(E_{un} H_{un}^* T - 1 + (E_{un} H_{un}^* T + 1) E_{un} \mu \delta H_{un}^* \sin(\omega T) \frac{\text{Re}\left(\frac{\partial \lambda}{\partial E}(E_{un}) z\right)}{\text{Re}\left(\frac{\partial \lambda}{\partial E}(E_{un})\right)} \right),$$

with $z = \left(E_{un} \mu \delta H_{un}^* \sin(\omega T) + \omega(\mu \delta - 4\omega^2 + 2(\mu + \delta)\omega i) e^{\omega(2-T)i} \right)^{-1}$. The parenthesis does not vanish because $2\omega i$ is not a solution of the characteristic equation (3.6).

3.5.2 Computation of the limit cycle

For instance, if $\tilde{\mu} = 0.233875$, $\tilde{\delta} = 0.361575$, $\tilde{T} = 1.7096$, $\tilde{E} = 0.08$, $B = 44$, $b = 3$, and $M = 4$, the equilibrium is already unstable since the linearization has an eigenvalue with real part $\text{Re}(\lambda) = 0.0387 > 0$. These values of the parameters are not too far from the reference values used in [19] and [8]. The corresponding nondimensional parameters are: $\mu = 0.9355$, $\delta = 1.4463$, $T = 0.4274$ (we have taken the values that minimize the function E_{un}), and $E = 675.84$.

In this example, the total populations of virgin mictic females and haploid males at equilibrium are $V^* = 0.1419$ and $H^* = 0.01125$ respectively, and the critical value is $E_{un} = 501.832$. Figure 3.3 shows the asymptotically stable limit cycle in the plane of total populations, with an estimated period $\frac{2\pi}{\omega} = 3.9163$ and an estimated radius $\sqrt{\frac{E-E_{un}}{E_2}} = 0.019$, since the coefficient $E_2 = 482005 > 0$ (direction of the bifurcation).

3.6 Numerical simulations

In addition to the analytical computations done until now, we have designed an explicit numerical scheme (mainly based on both analytical and numerical integration along characteristics) in order to compute the asymptotic behaviour of the solution of the system from a given initial conditions. In particular we have obtained a numerical approximation to the isolated periodic orbit. A successful application for this problem of an implicit numerical scheme has been developed by Angulo and López-Marcos in [6]. A more detailed revision on the numerical integration of age-structured population models can be found in [1] and for size-structured models we refer to [2].

First of all, we realize that if we know the solution of the *projected* system (3.11) $v(a, t) |_{0 \leq a \leq 1}$, $V_1(t)$, $H(t)$ with initial conditions $v^0(a) |_{0 \leq a \leq 1}$, V_1^0 , H^0 , we can compute the solution of the *centered at the origin* system (3.5), the *nondimensionalized* one (3.2) – (3.3) and the *original* one (3.1) with related initial conditions.

Indeed, the solution of system (3.5) is recovered integrating along the characteristic curves (straight parallel lines with slope 1):

$$h(a, t) = \begin{cases} h^0(a-t) e^{-\delta t} & a \geq t \\ V_1(t-a) e^{-\delta a} & a < t, \end{cases}$$

with an initial condition $h^0(a)$ such that $\int_0^\infty h^0(x) dx = H^0$ and

$$v(a, t) |_{a \geq 1} = \begin{cases} v^0(a-t) e^{-\mu t} & a-1 \geq t \\ v(1, t-(a-1)) e^{-\mu(a-1)} & a-1 < t, \end{cases}$$

with an initial condition $v^0(a) |_{a \geq 1}$ such that $\int_1^\infty v^0(x) dx = V_1^0$.

The solution of system (3.2) – (3.3) is easily obtained by adding the equilibrium to the solution

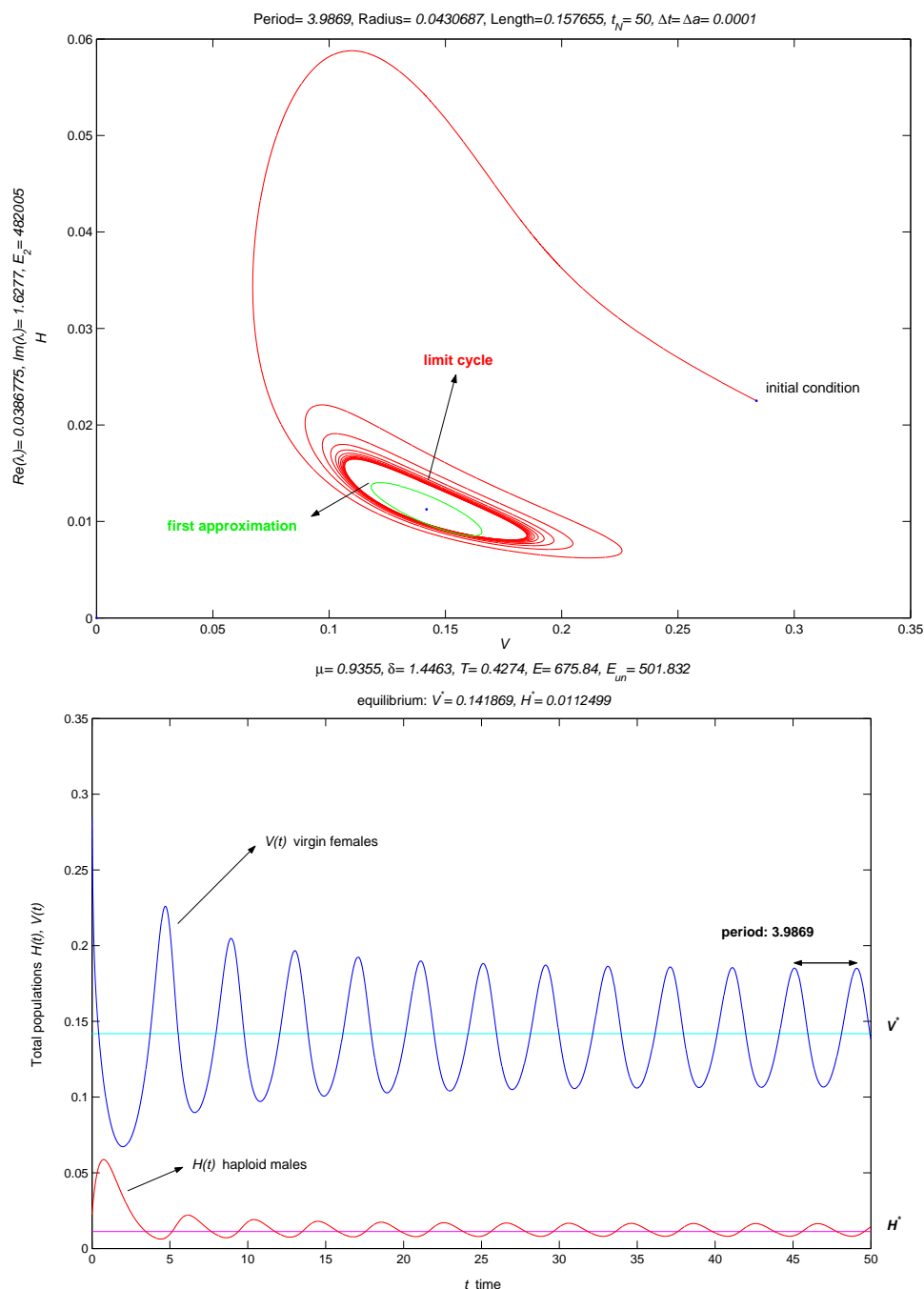


Figure 3.4: Numerical simulation from a “far” initial condition to the stable periodic orbit (taking the values of μ, δ, T that minimize the instability threshold value E_{un} , see Section 3.4.1). Top: the picture shows the orbit $(V(t), H(t))$ and a first approximation (see Figure 3.3) around the unstable equilibrium (V^*, H^*) in the plane of female and male population sizes. Bottom: both population sizes over time. λ is an eigenvalue with positive real part, and $E_2 > 0$ is a coefficient of the Hopf bifurcation. See Section 3.6 for further details.

of system (3.5):

$$\begin{aligned}\overbrace{v(a, t)}^{\text{old}} &= v^*(a) + v(a, t) \\ \overbrace{h(a, t)}^{\text{old}} &= h^*(a) + h(a, t),\end{aligned}$$

with initial conditions $\overbrace{v^0(a)}^{\text{old}} = v^*(a) + v^0(a)$, $\overbrace{h^0(a)}^{\text{old}} = h^*(a) + h^0(a)$. The solution of original system (3.1) is also easily obtained by rescaling the units of age, time and population (see Section 3.2.1):

$$\begin{aligned}\tilde{v}(\alpha, \tau) &= B \overbrace{v(a, t)}^{\text{old}} \\ \tilde{h}(\alpha, \tau) &= B b M \overbrace{h(a, t)}^{\text{old}},\end{aligned}$$

with initial conditions $\tilde{v}^0(\alpha) = B \overbrace{v^0(a)}^{\text{old}}$, $\tilde{h}^0(\alpha) = B b M \overbrace{h^0(a)}^{\text{old}}$. Finally, adding the first and second equations in (3.1) and integrating along the characteristic curves again, we get

$$m(\alpha, \tau) = -\tilde{v}(\alpha, \tau) + \begin{cases} (\tilde{v}^0(\alpha - \tau) + m^0(\alpha - \tau)) e^{-\mu\tau} & \alpha \geq \tau \\ B e^{-\mu\alpha} & \alpha < \tau, \end{cases}$$

with initial condition $m^0(\alpha)$ for the density of mated females. So, the original solution $\tilde{v}(\alpha, \tau)$, $m(\alpha, \tau)$, $\tilde{h}(\alpha, \tau)$ has been reached.

According to the formulas stated above, we only need to solve the *projected* system (3.11), that we rewrite in four equations (for latter numerical purposes) splitting first equation in two parts:

$$\left\{ \begin{array}{ll} \dot{v} + v' &= -(C_0 + EH)v - EHv^* & a \in (0, T) \\ \dot{v} + v' &= -\mu v & a \in (T, 1) \\ \dot{V}_1 &= v(1, t) - \mu V_1 \\ \dot{H} &= V_1 - \delta H \end{array} \right. \quad (3.12)$$

$$v(0, t) = 0, v(T^+, t) = v(T^-, t),$$

$$v(\cdot, 0) = v^0, V_1(0) = V_1^0, H(0) = H^0 \quad \text{initial conditions,}$$

where $C_0 = \mu + EH^*$ is a constant, and here $v^*(a) = e^{-C_0 a}$. Notice that the second boundary condition is the continuity of the solution at age T expressed in terms of right and left limits. This form of the system consists in a pair of (local) first-order hyperbolic partial differential equations and a pair of first-order ordinary differential equations. The first equation is not linear, but it

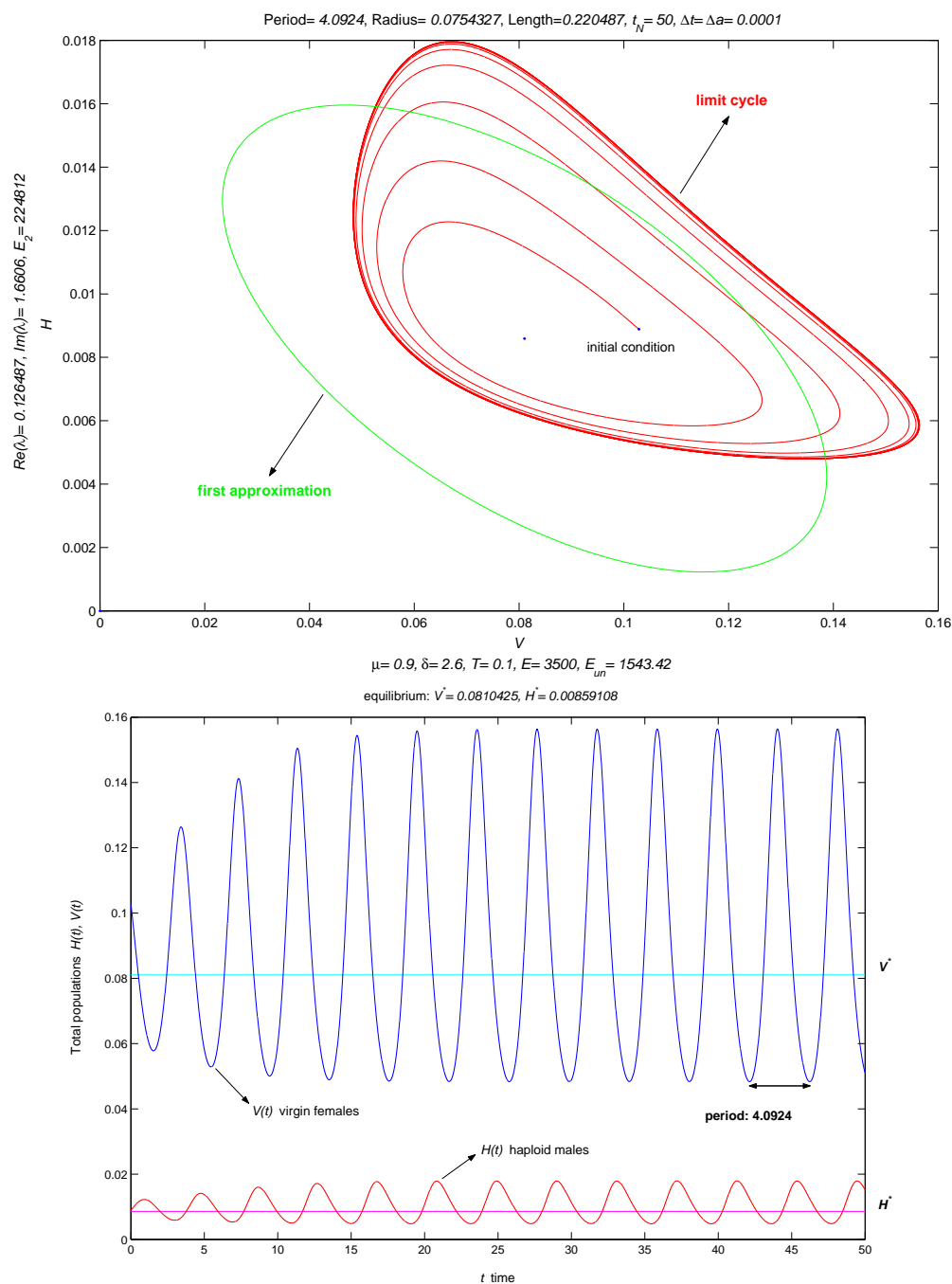


Figure 3.5: Numerical simulation from a “near” initial condition to the stable periodic orbit, for the case of a parameter values far away from the Hopf bifurcation values, i.e. $E \gg E_{un}$. See Section 3.6 and Figure 3.4 for further details.

becomes *inhomogeneous linear* if the variable H is given (prescribed) as a function of time. The other equations are linear. Therefore, taking the latter into account, equations (3.12) can be *solved implicitly* (in terms of integrals of the solution) integrating along characteristic curves the pde's and applying the *variation of the constants* (or variation of the parameters) formula to the ode's.

Indeed, let c be a constant and $\nu(t) := v(t+c, t)$ for $t \geq t_c := \max\{0, -c\}$, then the equation for ν is a first-order inhomogeneous linear ode (for given H) and the "solution" by the variation of the constants formula is

$$\nu(t) = e^{-\int_{t_c}^t C_0 + EH(s) ds} \nu(t_c) - \int_{t_c}^t e^{-\int_s^t C_0 + EH(\sigma) d\sigma} EH(s) \nu^*(s+c) ds,$$

which can be simplified using the Fundamental Theorem of Calculus. We solve the other equations in a similar way to obtain an *implicit representation of the solution* of (3.12) as follows:

$$\begin{aligned} v(a, t) \Big|_{0 \leq a \leq T} &= \begin{cases} v^0(a-t) e^{-\int_0^t C_0 + EH(s) ds} + v^*(a) (e^{-\int_0^t EH(s) ds} - 1) & a \geq t \\ v^*(a) (e^{-\int_{t-a}^t EH(s) ds} - 1) & a < t, \end{cases} \\ v(a, t) \Big|_{T \leq a \leq 1} &= \begin{cases} v^0(a-t) e^{-\mu t} & a - T \geq t \\ v(T, t - (a - T)) e^{-\mu(a-T)} & a - T < t, \end{cases} \\ V_1(t) &= e^{-\mu t} V_1^0 + \int_0^t e^{-\mu(t-s)} v(1, s) ds, \\ H(t) &= e^{-\delta t} H^0 + \int_0^t e^{-\delta(t-s)} V_1(s) ds. \end{aligned} \tag{3.13}$$

Notice that the second expression above for the density of females, $v(a, t) \Big|_{T \leq a \leq 1}$, has no integral terms and it is just computed from its initial condition and the density of T -aged females.

3.6.1 Implementation

Our aim is to obtain a numerical approximation to the solution, using the form (3.13), on a fixed time interval $[0, \bar{t}]$. We recall that the age domain is the (finite) interval $[0, 1]$. We construct a square grid on the rectangle domain $[0, 1] \times [0, \bar{t}]$ of the age-time space such that contains the points of age $a = T \leq 1$, the threshold age of fertilization.

Given a positive integer J , we define $\Delta a = \frac{1}{J}$ (age step), $\Delta t = \Delta a$ (time step), $N = \bar{t} J$ (number of discrete time levels), and the grid points $\{(a_j, t_n) : 0 \leq j \leq J, 0 \leq n \leq N\}$ with $a_j = j \Delta a$ and $t_n = n \Delta t$. We take Δa to be such that $I = \frac{T}{\Delta a} \in \mathbb{N}$. So, let $0 < I \leq J$ be the index of age

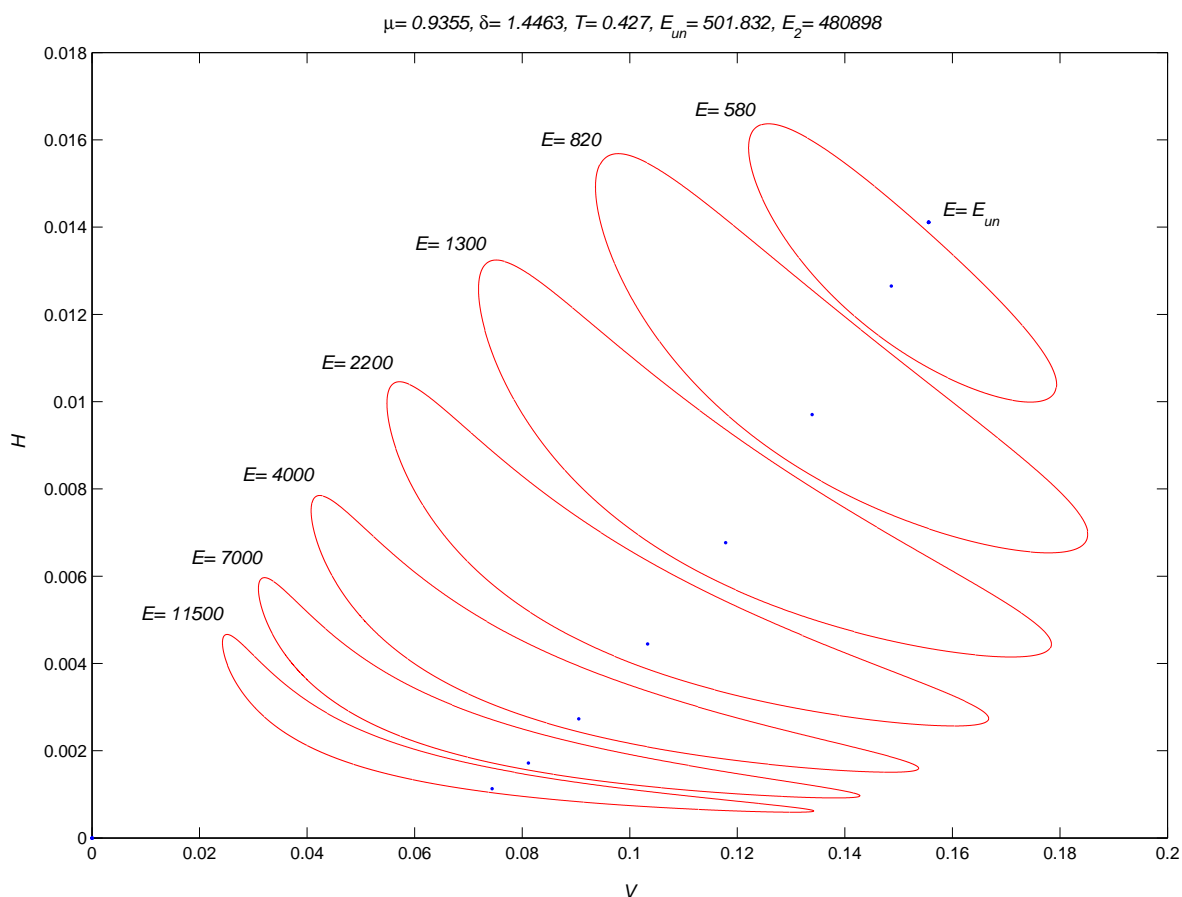


Figure 3.6: The limit cycle for several values ($501.832 = E_{un}$, 580, 820, 1300, 2200, 4000, 7000 and 11500) of the parameter E . The period of the orbit is an increasing function of E whereas the length of the orbit attains a maximum value.

T , i.e. $a_I = T$. We refer to the age a_j by a subscript j , and to the time level t_n by a superscript n . Let $v_j^n \simeq v(a_j, t_n)$, $V_1^n \simeq V_1(t_n)$, $H^n \simeq H(t_n)$ be an approximation to the solution at the grid points and let $v_j^* = v^*(a_j)$ be the females at equilibrium. Notice that, superscript 0 refers to the initial conditions: $v_j^0 = v^0(a_j)$, $V_1^0 = V_1(0)$, $H^0 = H(0)$ and subscript 0 refers to the boundary condition: $v_0^n = 0$. Expressions in (3.13) involving integrals can be written in a more suitable way:

$$\begin{aligned}
v(a, t + \Delta t) \Big|_{a \leq T} &= v(a - \Delta a, t) e^{-\int_t^{t+\Delta t} C_0 + EH(s) ds} + v^*(a) \left(e^{-\int_t^{t+\Delta t} EH(s) ds} - 1 \right), \\
V_1(t + \Delta t) &= e^{-\mu \Delta t} \left(V_1(t) + \int_t^{t+\Delta t} e^{-\mu(t-s)} v(1, s) ds \right), \\
H(t + \Delta t) &= e^{-\delta \Delta t} \left(H(t) + \int_t^{t+\Delta t} e^{-\delta(t-s)} V_1(s) ds \right),
\end{aligned} \tag{3.14}$$

where now all the integrals are over an interval of length Δt . The explicit numerical scheme proposed is a discretization of the solution formally obtained by the method of characteristics, where the integral terms have been substituted by a quadrature formulae. For $0 \leq n \leq N - 1$,

$$\begin{aligned}
&\left. \begin{aligned} \bar{V}_1^{n+1} &= e^{-\mu \Delta t} (V_1^n + \Delta t v_J^n) \\ \bar{H}^{n+1} &= e^{-\delta \Delta t} (H^n + \frac{\Delta t}{2} V_1^n) + \frac{\Delta t}{2} \bar{V}_1^{n+1} \end{aligned} \right\} \text{auxiliary values} \\
v_j^{n+1} &= v_{j-1}^n e^{-C_0 \Delta t - \frac{E \Delta t}{2} (H^n + \bar{H}^{n+1})} + v_j^* (e^{-\frac{E \Delta t}{2} (H^n + \bar{H}^{n+1})} - 1) \quad j=1, \dots, I \\
v_J^{n+1} &= \begin{cases} v_{J-n-1}^0 e^{-\mu(n+1)\Delta t} & J-I \geq n+1 \\ v_I^{n+1+I-J} e^{-\mu(1-T)} & J-I < n+1 \end{cases} \\
V_1^{n+1} &= e^{-\mu \Delta t} (V_1^n + \frac{\Delta t}{2} v_J^n) + \frac{\Delta t}{2} v_J^{n+1} \\
H^{n+1} &= e^{-\delta \Delta t} (H^n + \frac{\Delta t}{2} V_1^n) + \frac{\Delta t}{2} V_1^{n+1},
\end{aligned}$$

and the values v_j^{n+1} for $j = I + 1, \dots, J - 1$ are computed directly from (3.13). The scheme is explicit because there is only one unknown value (for each expression) at the new time level.

Assuming that the solution is sufficiently smooth in time, the local discretization error (local truncation error, i.e. the error produced by the method in one time step) is $\mathcal{O}(\Delta t^3)$. Indeed, the local error for the variables $V_1(t)$ and $H(t)$ is of order 3 since we have applied the trapezoidal rule in (3.14). For $v(a, t)$, $0 \leq a \leq T$, we have also used the trapezoidal rule, but with two additional values: \bar{V}_1^{n+1} and \bar{H}^{n+1} which are approximations using the rectangle rule and trapezoidal rule respectively. So, the resulting local error is $\mathcal{O}(\Delta t^3)$ too.

There are several explicit and implicit methods in the literature, however we have used an *ad hoc* numerical method instead of a general one mainly because the integration of the equations is partly done analytically, and then many terms in the scheme have no error. Other reasons are that the method is explicit and is not difficult to implement in a computer.

We have carried out several numerical experiments with the explicit scheme presented here,

taking different initial conditions and different values of the parameters. From a numerical point of view, we have checked some features of the solution, i.e., there is numerical evidence that:

- (i) the equilibrium solution is actually globally asymptotically stable when it is locally asymptotically stable.
- (ii) the limit cycle also exists for parameter values far away from the Hopf bifurcation values and it remains asymptotically stable.
- (iii) the local stability of the periodic orbit, when it exists, is actually global (except at the equilibrium point, of course).
- (iv) the *first approximation* (a particular eigenfunction, see Section 3.5.2) and the periodic orbit are sufficiently close in all studied cases.
- (v) the period of the oscillations is increasing as a function of the parameter E and the length of the orbit, seen as a closed curve in the plane, attains a maximum value with respect to E .

Thanks to the stability, for values of time large enough the solution orbit *catches* the limit cycle when it exists ($E > E_{un}$). In this case, we have also computed the period, the radius (i.e. the maximum distance to the equilibrium) and the length of the orbit in the plane of total populations females vs. males: $V(t), H(t)$ as old variables (see the beginning of Section 3.6). For the sake of completeness, we recall here that the relation between old and new variables is:

$$\begin{aligned} \overbrace{V(t)}^{\text{old}} &= V^* + V(t) = V^* + \int_0^1 v(x, t) dx + V_1(t) \\ \overbrace{H(t)}^{\text{old}} &= H^* + H(t) \end{aligned}$$

We summarize the obtained numerical results in the following pictures.

The first example, shown in Figure 3.4, corresponds to the parameter values that minimize the function E_{un} (instability threshold). We have taken an initial condition with population size larger than the population size of the equilibrium. Second example, depicted in Figure 3.5, shows the existence of the periodic oscillation for a parameter values far away from the Hopf bifurcation values, i.e. $E \gg E_{un}$, and we have chosen an initial condition close to the equilibrium point.

Finally, we have increased the parameter value E in order to know what happens to the system, at least numerically. The outcome is that no other bifurcation appears to the limit cycle which

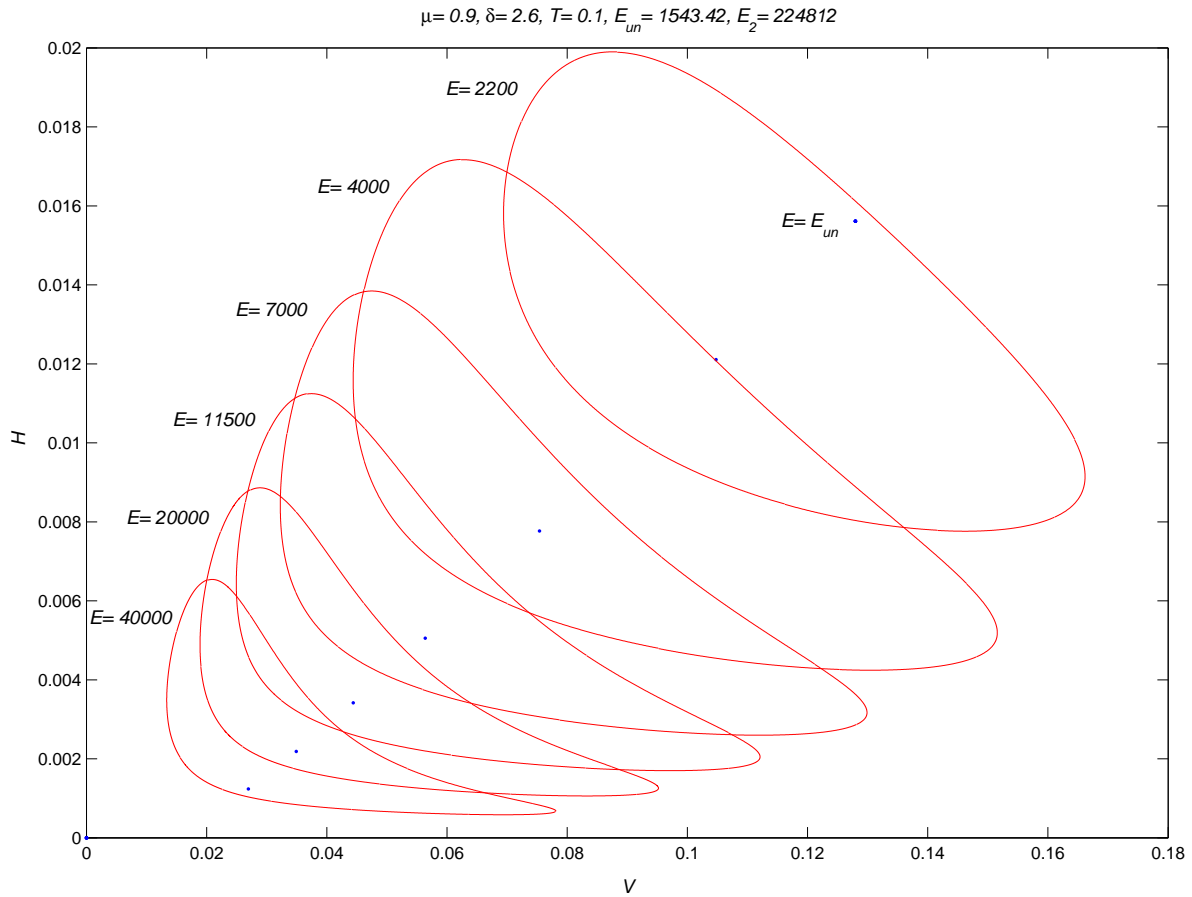


Figure 3.7: The limit cycle for different values ($1543.42 = E_{un}$, 2200, 4000, 7000, 11500, 20000 and 40000) of the parameter E . See also Figure 3.6.

remains asymptotically stable. Two examples are shown in Figures 3.6 and 3.7. On the one hand, the oscillation increases with E and on the other hand, the length of the closed orbit, in the plane of female-male, increases and decreases attaining a (local) maximum value with respect to E .

3.7 Sex-ratio

The Cyclic Parthenogenesis, such as in rotifers, provides a valuable model for the study of the evolution of sex-ratio. During their sexual phase, the appropriated definition of sex-ratio is the proportion between resting egg-producing females and male-producing females, i.e. the proportion between total mature mated females and total mature virgin females. See e.g. [8] and [9].

The sex-ratio when the population is at equilibrium equals to

$$\text{sex-ratio} = \frac{\overline{M}_1^*}{V_1^*} = \frac{e^{-\mu}}{\mu \delta H^*} - 1$$

whereas the sex-ratio when the population is in periodic motion with period p turns out to be

$$\text{sex-ratio} = \frac{e^{-\mu}}{\mu \delta p^{-1} \int_0^p H(s) ds} - 1$$

Notice that the sex-ratio is expressed in terms of the mortality rates and the number of haploid males. In [19], the authors obtained the relation among the parameters of the model that is favoured by the natural selection. The translation of their result into the nondimensional parameters is $0 < T = \ln(4) \mu e^\mu \delta E^{-1} \leq 1$, or $T = 1$ if the latter inequality does not hold.

In a future work we plan to (numerically) study some evolutionary aspects of the model when the population is in stable periodic motion.

Appendix A

Principle of Linearized stability for non-linear equations

SEVERAL AUTHORS have studied *principles of linearized stability* at equilibrium states for Cauchy problems in Banach spaces (specially for the case of semilinear equations), see e.g. [55], [36], or G.F. Webb in [67] (section 3). In essence, these principles establish a relationship between the stability of equilibrium solutions and the stability of the associated linearized system. In the literature of structured population dynamics several linearization principles can be found for semilinear equations and for some special non-linear equations, see for instance [74] and [53], and the references therein.

Recently some considerable extensions of these linearized stability results have appeared, see [68] W.M. Ruess 2003.

In this appendix we are going to state a general principle of linearized stability, for a class of non-linear evolution¹ equations involving *accretive operators* in Banach spaces. These operators, which are in general multivalued, are an extension of the monotone operators in Hilbert spaces. The prototype evolution equation is $\dot{u}(t) + Au(t) \ni F(u(t))$, $t \geq 0$, $u(0) = u^0 \in \overline{\mathcal{D}(A)}$ in a Banach space X , where we assume that:

- $A \subset X \times X$ (or $A : \mathcal{D}(A) \subset X \longrightarrow 2^X$) is a m -accretive, possibly multivalued, operator.
- $F : \overline{\mathcal{D}(A)} \longrightarrow X$ is a locally Lipschitz continuous operator.
- There exists an equilibrium solution $u^* \in \mathcal{D}(A)$, i.e. such that $Au^* \ni F(u^*)$.

¹In this context, evolution means evolution in ecological time.

- A is a resolvent-differentiable at u^* operator such that $A'(u^*)$ is a linear α -m-accretive operator for some real α .
- F is a Fréchet-differentiable at u^* operator. ($F'(u^*)$ is a bounded linear operator).

For this class of evolution equations, existence and uniqueness of *mild solutions* and a principle of linearized stability for stationary solutions has been obtained (see [68]). In this appendix we focus on the stability of equilibria which can be determined by means of the accretiveness of a certain associated linear operator.

The result can be applied to a general problem of age-dependent population dynamics, namely,

$$\frac{\partial}{\partial t}u(t) + \frac{\partial}{\partial a}u(t) = F(u(t)), \quad u(t)|_{a=0} = \mathbf{B}(u(t)), \quad t \geq 0, \quad u(0) = u^0$$

in the Banach space $X = L^1(0, \infty; \mathbb{R}^n)$ equipped with the norm $\|\phi\|_{L^1} = \sum_{i=1}^n \int_0^\infty |\phi_i(x)| dx$, with suitable conditions on the operator $\mathbf{B} : X \rightarrow \mathbb{R}^n$ (*birth function*), F being defined as before (*aging function*), and choosing an appropriate densely-defined and single-valued operator $A : \mathcal{D}(A) \subset X \rightarrow X$ for this equation (see below). In particular, we will obtain a principle of linearized stability for the *reduced system* (2.9) studied in Chapter 2.

A.1 Accretive operators in Banach spaces

In 1967 F.E. Browder [17] and T. Kato [54], independently, introduced the class of accretive operators, which arose as an extension of the well-known class of monotone operators in Hilbert spaces. This latter family became an important source for the development of the theory of elliptic partial differential equations, variational problems, resonance problems, as well as network problems. Classical examples of accretive operators include the gradient of a convex functional and the negative of the Laplacian operator defined in an appropriate domain, see for instance [11] V. Barbu. This theory has been found to be intimately related to the class of nonexpansive maps, which constitutes one of the families of mappings for which fixed-point results can be proved under the absence of the compactness assumption while placing emphasis on the geometric structure.

Throughout this appendix, X will denote a real Banach space equipped with a norm denoted by $\|\cdot\|$, where we will often deal with multivalued operators which can be viewed as subsets of the cartesian product space $A \subset X \times X$, or as set-valued maps $A : \mathcal{D}(A) \subset X \rightarrow 2^X$.

First of all, let us introduce the concepts of accretive, m-accretive, ω -accretive, and ω -m-accretive operator, as well as the definition of the resolvent operator and some of its properties that will be used later on.

A subset $A \subset X \times X$ (equivalently a multivalued operator from X to itself) is said to be accretive ² in X if for each $\lambda > 0$ and each pair $(x, y) \in A, (\bar{x}, \bar{y}) \in A$, we have

$$\|x - \bar{x} + \lambda(y - \bar{y})\| \geq \|x - \bar{x}\| . \quad (\text{A.1})$$

If, in addition, $\text{Range}(I + \lambda A) = X$ for all $\lambda > 0$, where I is the identity operator in X , then A is called m -accretive in X . If ω is any real number, a multivalued operator $A \subset X \times X$ for which $(A + \omega I)$ is accretive will be called ω -accretive, and ω - m -accretive if, in addition, $\text{Range}(I + \lambda A) = X$ for all $\lambda > 0$ with $\lambda\omega < 1$. If $A \subset X \times X$ is ω -accretive ³, then, for any $\lambda > 0$ with $\lambda\omega < 1$,

$$J_\lambda^A := (I + \lambda A)^{-1}$$

will denote the *resolvent operator* of A . From (A.1) it is easy to see that the resolvent is always a single-valued operator.

For the class of m -accretive operators A , some of the main properties of J_λ^A are given below (see for instance [11], chapter II):

1. the resolvent J_λ^A is a nonexpansive map defined in the whole Banach space, i.e.

$$\|J_\lambda^A y - J_\lambda^A \bar{y}\| \leq \|y - \bar{y}\| \text{ for all } y, \bar{y} \in X.$$
2. $\|J_\lambda^A x - x\| \leq \lambda \inf \{\|y\| : y \in Ax\}$ for all x in the domain of A (denoted by $\mathcal{D}(A)$), so

$$\lim_{\lambda \rightarrow 0} J_\lambda^A x = x \text{ for all } x \in \mathcal{D}(A).$$
3. if $\overline{\mathcal{D}(A)} = X$ (where the bar stands for its closure in X), $\lim_{\lambda \rightarrow 0} J_\lambda^A x = x$ for all $x \in X$ follows from 1 and 2 by density.

See also [14] H. Brézis, chapter VII, for similar results on linear accretive operators in Hilbert spaces. Now we state a theorem (principle of linearized stability for non-linear evolution equations involving accretive operators) we will use in the forthcoming.

Theorem A.1 ([68] W.M. Ruess, Corollary 3.2). *Let X be a real Banach space, let $A \subset X \times X$ be a m -accretive multivalued operator with domain $\mathcal{D}(A)$ such that $r \cdot \overline{\mathcal{D}(A)} \subset \overline{\mathcal{D}(A)}$ for $0 \leq r \leq 1$, and let $F : \overline{\mathcal{D}(A)} \rightarrow X$ be Lipschitz continuous on bounded sets. Consider an equilibrium solution u^* of the following initial value problem*

$$\begin{cases} \dot{u}(t) + Au(t) \ni F(u(t)), t \geq 0 & , \quad Au^* \ni F(u^*), u^* \in \mathcal{D}(A). \\ u(0) = u^0 \in \overline{\mathcal{D}(A)} \end{cases} \quad (\text{A.2})$$

²We say that A is dissipative if and only if $-A$ is accretive.

³Notice that an accretive operator is in particular a 0-accretive operator.

Assume that there exists $\tilde{A} \subset X \times X$ a multivalued linear operator that is α - m -accretive for some $\alpha \in \mathbb{R}$, and that there exists $\tilde{F} : X \rightarrow X$ a bounded linear operator that is a $\mathcal{D}(A)$ -Fréchet derivative of F at u^* , i.e. for any $\epsilon > 0$, there exists $\delta > 0$ such that, if $\phi \in \mathcal{D}(A)$, $\|\phi - u^*\| < \delta$ then $\|F(\phi) - F(u^*) - \tilde{F}(\phi - u^*)\| \leq \epsilon \|\phi - u^*\|$. The corresponding linearized equation is

$$\begin{cases} \dot{v}(t) + \tilde{A}v(t) \ni \tilde{F}v(t), & t \geq 0 \\ v(0) = v^0 \in \overline{\mathcal{D}(\tilde{A})} \end{cases} .$$

Furthermore, assume that A is resolvent-differentiable at u^* , in the sense that for every $\epsilon > 0$, there exist $\delta, \lambda_1 > 0$ and $\eta : (0, \lambda_1) \times X \rightarrow \mathbb{R}_+$ such that: if $\psi \in X$, $\|\psi - u^*\| < \delta$ then $\|J_\lambda^A \psi - J_\lambda^A u^* - J_\lambda^{\tilde{A}}(\psi - u^*)\| \leq \epsilon \lambda \|\psi - u^*\| + \lambda \eta(\lambda, \psi)$, for $0 < \lambda < \lambda_1$, and the function η is bounded on bounded sets, continuous in ψ , and $\lim_{(\lambda, \bar{\psi}) \rightarrow (0, \bar{\psi}_0)} \eta(\lambda, \bar{\psi}) = 0$.

Under the previous assumptions, if the ‘linearized’ operator $(\tilde{A} - \tilde{F} - \tilde{\omega}I)$ is accretive for some $\tilde{\omega} > 0$, then the Cauchy problem in (A.2) is locally exponentially stable at the equilibrium u^* . More precisely, for any $0 < \omega_1 < \tilde{\omega}$, there exists $\delta > 0$ such that, if $u^0 \in \overline{\mathcal{D}(A)}$, $\|u^0 - u^*\| < \delta$ then there exists a unique global mild solution $u(\cdot; u^0) : \mathbb{R}_+ \rightarrow X$ to the evolution equation in (A.2) such that $\|u(t; u^0) - u^*\| \leq e^{-\omega_1 t} \|u^0 - u^*\|$, for all $t \geq 0$.

We remark here that the operator A in Theorem A.1 can be any single-valued m -accretive operator in X that is $\mathcal{D}(A)$ -Fréchet-differentiable at the equilibrium. Obviously, Theorem A.1 also holds in particular if $A = \tilde{A} \subset X \times X$ is any linear m -accretive operator in X ; it need neither be single-valued, nor densely-defined. See [68] for further details. Unfortunately, this theorem does not give any criteria for the instability of the equilibrium solutions.

Our aim is to obtain a principle of linearized stability for the *reduced system* (2.9) of Chapter 2. To this end, we will apply Theorem A.1. So, first of all we have to show that this system, written as an evolution equation, takes the form of the abstract Cauchy problem in (A.2) for suitable operators A and F . To obtain the result, we will prove that the assumptions of Theorem A.1 are fulfilled by the pair of operators A and F .

Let us consider system (2.9) as a Cauchy problem in the Banach space $X = L^1(0, \infty; \mathbb{R})$ equipped with the usual norm denoted by $\|\cdot\|_1$, namely

$$\begin{cases} \frac{\partial}{\partial t} u(t) + \left(\frac{\partial}{\partial a} + \omega\right) u(t) = \left(\omega - \mu(\cdot, \int_0^\infty u(t) dx)\right) u(t), & t \geq 0, \\ u(t) \big|_{a=0} = B(u(t)), & t \geq 0, \\ u(0) = u^0 \in L^1, \end{cases} \quad (\text{A.3})$$

where the functional $\mathbf{B}(\phi) := \mathcal{B}((1-s)\phi, s\phi)$ and we assume Hypotheses 2.1–2.3 and 2.6 of Chapter 2. Notice that we have incorporated in the equation a linear term $\omega u(t)$ artificially. We assume further hypotheses,

Hypothesis A.1. There exists a non-trivial equilibrium solution $u^* \in W^{1,1}(0, \infty; \mathbb{R})$ of (A.3).

Here we recall that a function ϕ belongs to the Sobolev space $W^{1,1}$ if $\phi \in L^1$, and $\phi' \in L^1$ in the sense of distributions. In particular, ϕ is an absolutely continuous function.

Hypothesis A.2 (continuous Fréchet-differentiability). $\mathbf{B} : L^1 \rightarrow \mathbb{R}$ is continuously Fréchet-differentiable in an open neighbourhood of u^* , uniformly in the following sense:

there is $d > 0$ such that for each $\phi_0 \in L^1$, $\|\phi_0 - u^*\|_1 < d$ there exists $\mathbf{B}'(\phi_0)$, a bounded linear functional on L^1 , such that: for every $\epsilon > 0$, there exists $\delta > 0$ (independent of ϕ_0) such that, if $\phi \in L^1$, $\|\phi - \phi_0\|_1 < \delta$ then $|\mathbf{B}(\phi) - \mathbf{B}(\phi_0) - \mathbf{B}'(\phi_0)(\phi - \phi_0)| \leq \epsilon \|\phi - \phi_0\|_1$. Furthermore, the function $\phi_0 \mapsto \mathbf{B}'(\phi_0)$ is continuous.

The uniformity of $\delta > 0$ above, is a technical assumption that will be used in the proof of Proposition A.7.

Hypothesis A.3. \mathbf{B} is globally Lipschitz continuous, i.e. there exists $C_1 > 0$ such that:

$$|\mathbf{B}(\phi) - \mathbf{B}(\bar{\phi})| \leq C_1 \|\phi - \bar{\phi}\|_1, \text{ for all } \phi, \bar{\phi} \in L^1.$$

Hypothesis A.4. $\mu : [0, \infty) \times \mathbb{R} \rightarrow \mathbb{R}$ is such that $\mu(\cdot, 0) \in L^\infty(0, \infty; \mathbb{R})$, and there exists $D_2\mu(\cdot, \int_0^\infty u^* dx)$ which also belongs to $L^\infty(0, \infty; \mathbb{R})$.

Recall that a function φ belongs to $L^\infty(0, \infty; \mathbb{R})$ if it is essentially bounded, i.e. if there exists a constant c such that $|\varphi(x)| \leq c$ for almost all $x > 0$. L^∞ is a Banach space equipped with the norm $\|\varphi\|_\infty := \inf\{c : |\varphi(x)| \leq c \text{ a.e. } x > 0\}$. As usual, we identify L^∞ with the dual space of L^1 , the space of all continuous (bounded) linear functionals on L^1 .

Notice that, combining Hypotheses A.2 and A.3 it readily follows that $\|\mathbf{B}'(u^*)\|_\infty \leq C_1$. On the other hand, from Hypotheses 2.6 and A.4 it follows immediately that $\mu(\cdot, p) \in L^\infty$ for each $p \in \mathbb{R}$, since $|\mu(a, p)| \leq |\mu(a, 0)| + c_2(|p|)|p|$ for almost all $a \geq 0$.

We can write system (A.3) as the abstract Cauchy problem in (A.2) of the linearization theorem, with the operators $A : \mathcal{D}(A) \subset L^1 \rightarrow L^1$ and $F : L^1 \rightarrow L^1$ defined as:

$$\begin{cases} A\phi = \phi' + \omega\phi \\ \mathcal{D}(A) = \{\phi \in W^{1,1} : \phi(0) = \mathbf{B}(\phi)\} . \end{cases}$$

$$F(\phi) = \omega\phi - \mu(\cdot, \int_0^\infty \phi dx)\phi .$$

With regard to the operators in Theorem A.1, A is a single-valued non-linear operator (due to the non-linear boundary condition) and F is a non-linear operator defined in the whole Banach space.

Before stating next proposition, let us see a characterization of the accretiveness. In general, the condition to be accretive (A.1) for a multivalued operator, can be characterized in terms of the *normalized duality map*, see for instance [11]. For the particular case of a single-valued operator in L^1 , this characterization turns out to be

$$\langle \text{sign}(\phi - \bar{\phi}), A\phi - A\bar{\phi} \rangle \geq 0, \quad \text{for each pair } \phi, \bar{\phi} \in \mathcal{D}(A),$$

since in that case the normalized duality map is the signum function. The duality pairing between L^∞ and L^1 is denoted by $\langle \cdot, \cdot \rangle$ and it is defined as $\langle \varphi, \phi \rangle = \int_0^\infty \varphi(x) \phi(x) dx$.

Next proposition is devoted to the m -accretiveness of A . Namely, we have:

Proposition A.2. *Under the previous hypotheses,*

the operator $A : \mathcal{D}(A) \subset L^1 \longrightarrow L^1$ is m -accretive provided that $\omega \geq C_1$.

Proof. Taking the previous characterization of the accretiveness into account, the operator A is accretive (as long as $\omega \geq C_1 > 0$) since for each pair $\phi, \bar{\phi} \in \mathcal{D}(A)$ we have

$$\begin{aligned} \langle \text{sign}(\phi - \bar{\phi}), A\phi - A\bar{\phi} \rangle &= \langle \text{sign}(\phi - \bar{\phi}), (\phi - \bar{\phi})' + \omega(\phi - \bar{\phi}) \rangle = \\ &= \int_0^\infty |\phi - \bar{\phi}|' dx + \omega \|\phi - \bar{\phi}\|_1 = -|\phi(0) - \bar{\phi}(0)| + \omega \|\phi - \bar{\phi}\|_1 \geq (\omega - C_1) \|\phi - \bar{\phi}\|_1 \geq 0. \end{aligned}$$

Notice that we have used the condition of the domain of A combined with the hypothesis that B is globally Lipschitz continuous, that is $|\phi(0) - \bar{\phi}(0)| = |B(\phi) - B(\bar{\phi})| \leq C_1 \|\phi - \bar{\phi}\|_1$.

To prove that $\text{Range}(I + \lambda A) = L^1$ for all $\lambda > 0$, let $\psi \in L^1$ and consider the equation $\phi + \lambda A\phi = \psi$, i.e. the problem:

$$\begin{cases} \lambda \phi' + (1 + \lambda \omega) \phi = \psi, & a \geq 0, \\ \phi(0) = B(\phi). \end{cases} \quad (\text{A.4})$$

Let $\hat{\lambda} := \frac{1+\lambda\omega}{\lambda} > 0$. Applying the *variation of the constants* formula to the inhomogeneous linear first-order ordinary differential equation with constant coefficients in (A.4), we get

$$\phi(a) = e^{-\hat{\lambda}a} \left(\phi(0) + \int_0^a e^{\hat{\lambda}x} \frac{\psi(x)}{\lambda} dx \right), \quad (\text{A.5})$$

with $\phi(0) \in \mathbb{R}$ the unique solution of the scalar equation (the boundary condition in (A.4)):

$$\phi(0) = B \left(e^{-\hat{\lambda} \cdot} \left(\phi(0) + \int_0^\cdot e^{\hat{\lambda}x} \frac{\psi(x)}{\lambda} dx \right) \right). \quad (\text{A.6})$$

The latter follows from the fact that the right hand side of (A.6) is a contractive map regarded as a function of the independent variable $\phi(0)$. Indeed, let ϕ and $\bar{\phi}$ be two solutions of the first equation of (A.4) with different initial values $\phi(0)$ and $\bar{\phi}(0)$, using again the Lipschitzness of \mathbf{B} we have

$$|\mathbf{B}(\phi) - \mathbf{B}(\bar{\phi})| \leq C_1 \left\| e^{-\hat{\lambda} \cdot} (\phi(0) - \bar{\phi}(0)) \right\|_1 = \frac{C_1}{\hat{\lambda}} |\phi(0) - \bar{\phi}(0)| \leq \frac{\lambda \omega}{1 + \lambda \omega} |\phi(0) - \bar{\phi}(0)|.$$

Thus proving that the operator A is m-accretive. \square

The initial condition ($t = 0$) of system (A.3) belongs to X , the Banach space of reference, on the other hand the initial value of system (A.2) only belongs to the closure of the domain of A . However, both systems agree. Indeed, next statement concerns with the density of the domain $\mathcal{D}(A)$,

Proposition A.3. *Under the previous hypotheses, $\overline{\mathcal{D}(A)} = L^1$.*

The proof of this result can be found in [74] (PROPOSITION 3.8, page 89), where the positivity assumption is not essential. See also [10] (PROPOSITION 2.2, page 65) for the proof of a result with very similar hypotheses. Now we see that the condition appearing in the linearization theorem A.1, $r \cdot \overline{\mathcal{D}(A)} \subset \overline{\mathcal{D}(A)}$ for $0 \leq r \leq 1$, is trivially fulfilled.

The assumptions on the mortality rate μ imply that the operator F is also Lipschitz continuous on bounded sets. Namely we have,

Proposition A.4. *Under the previous hypotheses,*

there exists $C_2(r) > 0$ such that if $\|\phi\|_1, \|\bar{\phi}\|_1 \leq r$, then $\|F(\phi) - F(\bar{\phi})\|_1 \leq C_2(r) \|\phi - \bar{\phi}\|_1$.

Proof. Let $\phi, \bar{\phi} \in L^1$ such that $\|\phi\|_1, \|\bar{\phi}\|_1 \leq r$. Let $p = \int_0^\infty \phi dx$ and $\bar{p} = \int_0^\infty \bar{\phi} dx$, using the Lipschitzness of μ with respect to the second variable, we have

$$|\mu(a, p)| \leq |\mu(a, \bar{p})| + c_2(r) |p - \bar{p}| \leq |\mu(a, \bar{p})| + c_2(r) \|\phi - \bar{\phi}\|_1 \quad \text{for almost all } a \geq 0.$$

Therefore:

$$\begin{aligned} \|F(\phi) - F(\bar{\phi})\|_1 &= \|\omega(\phi - \bar{\phi}) - \mu(\cdot, p)\phi + \mu(\cdot, \bar{p})\bar{\phi}\|_1 \leq \\ &\leq \omega \|\phi - \bar{\phi}\|_1 + \|\mu(\cdot, p)(\phi - \bar{\phi}) + (\mu(\cdot, p) - \mu(\cdot, \bar{p}))\bar{\phi}\|_1 \leq \\ &\leq (\omega + \|\mu(\cdot, p)\|_\infty) \|\phi - \bar{\phi}\|_1 + \|\mu(\cdot, p) - \mu(\cdot, \bar{p})\|_\infty r \leq \\ &\leq (\omega + \|\mu(\cdot, 0)\|_\infty + c_2(r) \|\phi\|_1) \|\phi - \bar{\phi}\|_1 + c_2(r) |p - \bar{p}| r \leq \\ &\leq (\omega + \|\mu(\cdot, 0)\|_\infty + 2c_2(r)r) \|\phi - \bar{\phi}\|_1. \end{aligned}$$

So, F is locally Lipschitz continuous with constant $C_2(r) = \omega + \|\mu(\cdot, 0)\|_\infty + 2c_2(r)r > 0$. \square

The remainder of this appendix is devoted to checking the assumptions about the linearization procedure.

Let us consider the single-valued linear operator $\tilde{A} : \mathcal{D}(\tilde{A}) \subset L^1 \longrightarrow L^1$ defined by:

$$\begin{cases} \tilde{A}\phi = \phi' + \omega\phi \\ \mathcal{D}(\tilde{A}) = \{\phi \in W^{1,1} : \phi(0) = \langle \mathbf{B}'(u^*), \phi \rangle\}, \end{cases} \quad (\text{A.7})$$

where the bounded linear functional $\mathbf{B}'(u^*)$ is the Fréchet derivative of \mathbf{B} at u^* . Remember that by Hypothesis A.2, the functional \mathbf{B} is continuously Fréchet-differentiable in an open neighbourhood of u^* . Now we prove the α -m-accretiveness of \tilde{A} .

Proposition A.5. *Under the previous hypotheses,*

the linear operator $\tilde{A} : \mathcal{D}(\tilde{A}) \subset L^1 \longrightarrow L^1$ is α -m-accretive for $\alpha \geq (\|\mathbf{B}'(u^)\|_\infty - \omega)$.*

Here we remark that if we assume the restriction on ω in proposition A.2, then the lower bound on the constant α above is smaller than or equal to zero since $\omega \geq C_1 \geq \|\mathbf{B}'(u^*)\|_\infty$.

Proof. We have to show both that $\tilde{A} + \alpha I$ is accretive for some α and that $\text{Range}(I + \lambda \tilde{A}) = L^1$ for all $\lambda > 0$ with $\lambda\alpha < 1$. Proceeding as in the proof of Proposition A.2, we have that for $\alpha \geq \|\mathbf{B}'(u^*)\|_\infty - \omega$ and for each pair $\phi, \bar{\phi} \in \mathcal{D}(\tilde{A})$,

$$\begin{aligned} \langle \text{sign}(\phi - \bar{\phi}), (\tilde{A} + \alpha I)\phi - (\tilde{A} + \alpha I)\bar{\phi} \rangle &= \langle \text{sign}(\phi - \bar{\phi}), (\phi - \bar{\phi})' + (\alpha + \omega)(\phi - \bar{\phi}) \rangle = \\ &= \int_0^\infty |\phi - \bar{\phi}|' dx + (\alpha + \omega) \|\phi - \bar{\phi}\|_1 = -|\phi(0) - \bar{\phi}(0)| + (\alpha + \omega) \|\phi - \bar{\phi}\|_1 = \\ &= -\langle \mathbf{B}'(u^*), \phi - \bar{\phi} \rangle + (\alpha + \omega) \|\phi - \bar{\phi}\|_1 \geq (\alpha + \omega - \|\mathbf{B}'(u^*)\|_\infty) \|\phi - \bar{\phi}\|_1 \geq 0. \end{aligned}$$

Thus proving the first part. To prove the second part, let $\lambda > 0$ with $\lambda\alpha < 1$, let $\psi \in L^1$ and consider the equation $\phi + \lambda \tilde{A}\phi = \psi$, i.e. the linear problem:

$$\begin{cases} \lambda\phi' + (1 + \lambda\omega)\phi = \psi, & a \geq 0, \\ \phi(0) = \langle \mathbf{B}'(u^*), \phi \rangle. \end{cases} \quad (\text{A.8})$$

Setting $\hat{\lambda} = \frac{1+\lambda\omega}{\lambda}$ again, as in the proof of Proposition A.2, we get the explicit solution

$$\phi(a) = e^{-\hat{\lambda}a} \left(\phi(0) + \int_0^a e^{\hat{\lambda}x} \frac{\psi(x)}{\lambda} dx \right),$$

because this time $\phi(0) \in \mathbb{R}$ can be computed from the linear boundary condition in (A.8) as:

$$\phi(0) = \frac{\left\langle \mathbf{B}'(u^*), \int_0^\cdot e^{\hat{\lambda}(x-\cdot)} \frac{\psi(x)}{\lambda} dx \right\rangle}{1 - \langle \mathbf{B}'(u^*), e^{-\hat{\lambda}\cdot} \rangle} \quad (\text{A.9})$$

Notice that since $\alpha + \omega \geq \|B'(u^*)\|_\infty > 0$,

$$|\langle B'(u^*), e^{-\hat{\lambda} \cdot} \rangle| \leq \|B'(u^*)\|_\infty \|e^{-\hat{\lambda} \cdot}\|_1 = \frac{\|B'(u^*)\|_\infty}{\hat{\lambda}} = \frac{\lambda \|B'(u^*)\|_\infty}{1 + \lambda \omega} \leq \frac{\lambda(\alpha + \omega)}{1 + \lambda \omega} < 1.$$

Thus proving that the linear operator \tilde{A} is α -m-accretive. \square

Analogously to the operator A , the following proposition states that the operator \tilde{A} is densely-defined in X , the Banach space of reference. Namely we have,

Proposition A.6. *Under the previous hypotheses, $\overline{\mathcal{D}(\tilde{A})} = L^1$.*

The proof is analogous to the proof of Proposition A.3.

Finally, let us consider the bounded linear operator $\tilde{F} : L^1 \rightarrow L^1$ defined as:

$$\tilde{F} \phi = (\omega - \mu(\cdot, \int_0^\infty u^* dx)) \phi - D_2 \mu(\cdot, \int_0^\infty u^* dx) u^* \int_0^\infty \phi dx, \quad (\text{A.10})$$

that is, $\tilde{F} = F'(u^*)$ is the Fréchet derivative of F at u^* . According to Hypothesis A.4, $\mu(\cdot, p) \in L^\infty$ for each $p \in \mathbb{R}$, the map $p \mapsto \mu(\cdot, p)$ is differentiable at $p = \int_0^\infty u^* dx$ and $D_2 \mu(\cdot, \int_0^\infty u^* dx) \in L^\infty$.

The corresponding linearization of system (A.3), taking formally $u(t) \simeq u^* + v(t)$, is

$$\begin{cases} \frac{\partial}{\partial t} v(t) + \left(\frac{\partial}{\partial a} + \omega\right) v(t) = \tilde{F} v(t), & t \geq 0, \\ v(t)|_{a=0} = \langle B'(u^*), v(t) \rangle, & t \geq 0, \\ v(0) = v^0 \in L^1. \end{cases} \quad (\text{A.11})$$

Next proposition concerns with the resolvent-differentiability of A at the equilibrium.

Proposition A.7 (resolvent-differentiability of A at u^*). *Under the previous hypotheses and assuming $\omega \geq C_1$, the following holds:*

for every $\epsilon > 0$, there exist $\delta, \lambda_1 > 0$, and $\eta : (0, \lambda_1) \times L^1 \rightarrow \mathbb{R}_+$ such that: if $\psi \in L^1$, $\|\psi - u^\|_1 < \delta$ then $\left\| J_\lambda^A \psi - J_\lambda^A u^* - J_\lambda^{\tilde{A}}(\psi - u^*) \right\|_1 \leq \epsilon \lambda \|\psi - u^*\|_1 + \lambda \eta(\lambda, \psi)$, for $0 < \lambda < \lambda_1$, and the function η is bounded on bounded sets, continuous in ψ , and $\lim_{(\lambda, \bar{\psi}) \rightarrow (0, \bar{\psi}_0)} \eta(\lambda, \bar{\psi}) = 0$.*

Proof. Let us assume that $\omega \geq C_1$, where C_1 is the global Lipschitz constant of B , and let $\alpha \geq (\|B'(u^*)\|_\infty - \omega)$. We have by Propositions A.2 and A.5 that

$$\text{Range}(I + \lambda A) = \text{Range}(I + \lambda \tilde{A}) = L^1$$

for all $\lambda > 0$ with $\lambda < \lambda_0$, where $\lambda_0 := \frac{1}{\alpha}$, if $\alpha > 0$ and $\lambda_0 := \infty$, otherwise. So, let $0 < \lambda < \lambda_0$ and let $\psi \in L^1$.

On the one hand, for any $\psi \in L^1$ let us consider two images of the resolvent operator of A , namely, $J_\lambda^A \psi =: \phi$ and $J_\lambda^A u^* =: \phi^*$, or equivalently $(I + \lambda A) \phi = \psi$ and $(I + \lambda A) \phi^* = u^*$, respectively.

Let $\hat{\lambda} := \frac{1+\lambda\omega}{\lambda} > 0$, as in proof of Proposition A.2, ϕ and ϕ^* are given by:

$$\phi(a) = e^{-\hat{\lambda}a} \left(\phi(0) + \int_0^a e^{\hat{\lambda}x} \frac{\psi(x)}{\lambda} dx \right) \quad \text{with } \phi(0) = \mathbf{B}(\phi) \quad (\text{A.12})$$

and

$$\phi^*(a) = e^{-\hat{\lambda}a} \left(\phi^*(0) + \int_0^a e^{\hat{\lambda}x} \frac{u^*(x)}{\lambda} dx \right) \quad \text{with } \phi^*(0) = \mathbf{B}(\phi^*) . \quad (\text{A.13})$$

Recall that the values of $\phi(0)$ and $\phi^*(0)$ are uniquely determined through their corresponding scalar non-linear equations, see (A.6). Also remember that J_λ^A is a nonexpansive operator (see Property 1 at the beginning of the section), so we have that $\|\phi - \phi^*\|_1 \leq \|\psi - u^*\|_1$.

On the other hand, as in proof of Proposition A.5, let us also compute the resolvent operator of \tilde{A} evaluated at $\psi - u^* \in L^1$, i.e.

$$J_\lambda^{\tilde{A}}(\psi - u^*)(a) = e^{-\hat{\lambda}a} \left(J_\lambda^{\tilde{A}}(\psi - u^*)(0) + \int_0^a e^{\hat{\lambda}x} \frac{\psi(x) - u^*(x)}{\lambda} dx \right) , \quad (\text{A.14})$$

with $J_\lambda^{\tilde{A}}(\psi - u^*)(0) = \frac{\langle \mathbf{B}'(u^*), \int_0^\cdot e^{\hat{\lambda}(x-\cdot)} \frac{\psi(x) - u^*(x)}{\lambda} dx \rangle}{1 - \langle \mathbf{B}'(u^*), e^{-\hat{\lambda}\cdot} \rangle}$. Notice that $J_\lambda^{\tilde{A}}$ is a linear operator.

Before using Hypothesis A.2, let us see a useful relation coming from (A.12), (A.13) and (A.14), namely

$$\begin{aligned} & \mathbf{B}(\phi) - \mathbf{B}(\phi^*) - \langle \mathbf{B}'(u^*), \phi - \phi^* \rangle = \\ & = \phi(0) - \phi^*(0) - \left\langle \mathbf{B}'(u^*), e^{-\hat{\lambda}\cdot} (\phi(0) - \phi^*(0)) + \int_0^\cdot e^{\hat{\lambda}(x-\cdot)} \frac{\psi(x) - u^*(x)}{\lambda} dx \right\rangle = \\ & = (\phi(0) - \phi^*(0)) \left(1 - \langle \mathbf{B}'(u^*), e^{-\hat{\lambda}\cdot} \rangle \right) - \left\langle \mathbf{B}'(u^*), \int_0^\cdot e^{\hat{\lambda}(x-\cdot)} \frac{\psi(x) - u^*(x)}{\lambda} dx \right\rangle = \\ & = \left(1 - \langle \mathbf{B}'(u^*), e^{-\hat{\lambda}\cdot} \rangle \right) \left(\phi(0) - \phi^*(0) - J_\lambda^{\tilde{A}}(\psi - u^*)(0) \right) . \end{aligned}$$

Furthermore, taking the previous relation into account and combining again (A.12), (A.13) and (A.14), we get:

$$\begin{aligned} & \left\| J_\lambda^A \psi - J_\lambda^A u^* - J_\lambda^{\tilde{A}}(\psi - u^*) \right\|_1 = \left\| e^{-\hat{\lambda}\cdot} \left(\phi(0) - \phi^*(0) - J_\lambda^{\tilde{A}}(\psi - u^*)(0) \right) \right\|_1 = \\ & = \frac{1}{\hat{\lambda}} \left| \phi(0) - \phi^*(0) - J_\lambda^{\tilde{A}}(\psi - u^*)(0) \right| = \frac{|\mathbf{B}(\phi) - \mathbf{B}(\phi^*) - \langle \mathbf{B}'(u^*), \phi - \phi^* \rangle|}{\hat{\lambda} \left| 1 - \langle \mathbf{B}'(u^*), e^{-\hat{\lambda}\cdot} \rangle \right|} . \end{aligned} \quad (\text{A.15})$$

Now using that

$$\hat{\lambda} \left| 1 - \langle \mathbf{B}'(u^*), e^{-\hat{\lambda} \cdot} \rangle \right| \geq \hat{\lambda} \left(1 - \langle |\mathbf{B}'(u^*)|, e^{-\hat{\lambda} \cdot} \rangle \right) \geq \hat{\lambda} - \|\mathbf{B}'(u^*)\|_\infty \geq \hat{\lambda} - \omega = \frac{1}{\lambda}, \quad (\text{A.16})$$

we are ready to prove the resolvent-differentiability of A at u^* . Indeed, we will apply Hypothesis A.2 at the points $\phi_0 = J_\lambda^A u^* = \phi^*$ combined with (A.15) and (A.16). In order to do that, we see that by Property 2 of J_λ^A , there exists $\tilde{\lambda}_0 > 0$ small enough such that $\|\phi^* - u^*\|_1 < d$ for all $0 < \lambda < \lambda_1 := \min\{\lambda_0, \tilde{\lambda}_0\}$, where λ_0 is defined above. Then for every $\epsilon > 0$ there exists $\delta > 0$ (independent of λ) such that if $\|\phi - \phi^*\|_1 \leq \|\psi - u^*\|_1 < \delta$ then

$$\begin{aligned} \left\| J_\lambda^A \psi - J_\lambda^A u^* - J_\lambda^{\tilde{A}}(\psi - u^*) \right\|_1 &\leq \lambda |\mathbf{B}(\phi) - \mathbf{B}(\phi^*) - \langle \mathbf{B}'(u^*), \phi - \phi^* \rangle| = \\ &= \lambda |\mathbf{B}(\phi) - \mathbf{B}(\phi^*) - \langle \mathbf{B}'(u^*) + \mathbf{B}'(\phi^*) - \mathbf{B}'(\phi^*), \phi - \phi^* \rangle| \leq \end{aligned}$$

$$\leq \epsilon \lambda \|\phi - \phi^*\|_1 + \lambda |\langle \mathbf{B}'(u^*) - \mathbf{B}'(\phi^*), \phi - \phi^* \rangle| \leq \epsilon \lambda \|\psi - u^*\|_1 + \lambda \|\mathbf{B}'(u^*) - \mathbf{B}'(\phi^*)\|_\infty \|\psi - u^*\|_1,$$

for all $0 < \lambda < \lambda_1$. Finally, if we define the function $\eta : (0, \lambda_1) \times L^1 \rightarrow \mathbb{R}_+$ as follows,

$$\eta(\lambda, \psi) := \|\mathbf{B}'(u^*) - \mathbf{B}'(J_\lambda^A u^*)\|_\infty \|\psi - u^*\|_1,$$

which is bounded on bounded sets, continuous in ψ , and for any $\bar{\psi}_0 \in L^1$ $\lim_{(\lambda, \bar{\psi}) \rightarrow (0, \bar{\psi}_0)} \eta(\lambda, \bar{\psi}) = 0$, then the desired conclusion follows. Notice that the latter limit follows from two facts, namely, $\lim_{\lambda \rightarrow 0} J_\lambda^A u^* = u^*$, see Property 2 at the beginning of the section, and the mapping $\phi_0 \mapsto \mathbf{B}'(\phi_0)$ being continuous at $\phi_0 = u^*$, according to Hypothesis A.2. \square

We summarize these last results in the following

Theorem A.8 (of linearized stability for system (A.3) or (2.9) in Section 2.4). *Under Hypotheses 2.1–2.3, 2.6, A.1–A.4 and assuming $\omega \geq C_1$, if the ‘linearized’ operator $(\tilde{A} - \tilde{F} - \tilde{\omega} I)$ is accretive for some $\tilde{\omega} > 0$, then the Cauchy problem (A.3) is locally exponentially stable at the equilibrium u^* .*

More precisely, for any $0 < \omega_1 < \tilde{\omega}$, there exists $\delta > 0$ such that, if $u^0 \in L^1$, $\|u^0 - u^\|_1 < \delta$ then there exists a unique global mild solution $u(\cdot; u^0) : \mathbb{R}_+ \rightarrow L^1$ to the evolution equation (A.3) such that $\|u(t; u^0) - u^*\|_1 \leq e^{-\omega_1 t} \|u^0 - u^*\|_1$, for all $t \geq 0$.*

Appendix B

Summary in catalan

LA MODELITZACIÓ matemàtica té el seu propi lloc en totes les ciències. La tesi que teniu a les mans versa sobre models matemàtics de les ciències biològiques, o més ben dit, d'una petita àrea anomenada *dinàmica de poblacions estructurades*. L'objecte d'estudi d'aquesta matèria, com el seu propi nom indica, és l'evolució en el temps de poblacions biològiques (animals, cèl·lules ...) o de vegades també poblacions humanes, amb una *estructura interna* donada/definida per una o diverses variables, que generalment són característiques fisiològiques. De fet, aquesta estructura ens permet incorporar en els models la possible diversitat que podem observar en els individus de la població. Llavors, podríem dir que els individus són distinguits/diferenciats per aquestes variables d'estructura com poden ser l'edat, la mida (*tamaño/size*) del cos, el contingut de proteïnes, el sexe, la maduresa cel·lular, el fenotip, la posició en l'espai (essent en aquest cas, però, una variable externa), o qualsevol altre tret/factor que tingui un efecte significatiu en la (maduració), la supervivència, i la reproducció de l'espècie en consideració.

Sempre que el fenomen que ens interessi estudiar/analitzar/predir depengui de la diversitat que poden exhibir els individus que constitueixen una població, la visió (*approach*) de la dinàmica de poblacions estructurades pot resultar adequada i convenient.

Aquesta matèria s'origina a partir de models deterministes i sense estructura de dinàmica de poblacions per a una sola espècie, com poden ser l'equació de Malthus i l'equació *generalitzada* de Verhulst (una equació de Bernoulli). En temps continu, aquests models elementals prenen la forma d'una sola equació diferencial ordinària per a la mida de la població (població total), i alguns d'ells es poden solucionar/integrar explícitament mitjançant mètodes senzills com per exemple separant variables.

A tall d'exemple només, donem aquí una breu discussió dels dos exemples fonamentals citats

anteriorment. L'equació de Malthus prediu un creixement *exponencial* de la població. En efecte, considerant una població tancada, e.g. una sola espècie vivint en un hàbitat aïllat, i anomenant $N(t)$ a la mida de la població a temps t , es té que

$$N'(t) = r(t) N(t), \quad r(t) \text{ és la taxa de creixement intrínseca, } \quad N(t) = N(t_0) e^{\int_{t_0}^t r(s) ds}.$$

Per altra banda, l'equació de Bernoulli prediu un creixement *logístic* de la població, i.e. una convergència monòtona cap a un estat d'equilibri no trivial. En efecte, l'anterior equació lineal és modificada de manera que resulta la següent equació no lineal:

$$N'(t) = r(t) \left(1 - \left(\frac{N(t)}{K} \right)^\theta \right) N(t), \quad K > 0 \text{ és l'anomenada capacitat del medi, } \theta > 0,$$

i amb un canvi de variables ¹:

$$x = N^\theta, \quad \frac{dx}{dt} = \theta N^{\theta-1} \frac{dN}{dt}, \quad x(t) = \frac{K^\theta x(t_0)}{x(t_0) + (K^\theta - x(t_0)) e^{-\theta \int_{t_0}^t r(s) ds}}, \quad N(t) = (x(t))^{1/\theta}.$$

L'equació de Bernoulli i l'equació de Verhulst ($\theta = 1$), que és un cas particular de la primera, són probablement la manera més simple d'incorporar en el model els efectes dependents de la densitat de població com per exemple la competència pels recursos limitats. En general, els models de creixement de poblacions d'una sola espècie incorporant dependències entre els individus es poden descriure mitjançant una equació no lineal de la forma $N'(t) = F(t, N(t)) N(t)$, amb una definició convenient de la funció F .

Malgrat la seva simplicitat, ambdós sistemes són models paradigmàtics des del punt de vista de la modelització, encara que cal remarcar que no tracten explícitament el fenomen de la reproducció sexual. Vegeu per exemple el llibre de J.D. Murray ([61], volum I, capítols 1 i 2) per a una bona introducció a models bàsics de poblacions. Vegeu també el recent llibre de H.R. Thieme 2003 [72] el qual cobreix (descriu/analitza) un ampli ventall de models de dinàmica de poblacions.

En paraules de Thieme, es podria dir que la biologia, la ciència de la vida, ha desenvolupat els seus propis models 'no matemàtics', però últimament la formulació de la dinàmica de poblacions en termes d'equacions (matemàtiques), l'anàlisi d'aquestes equacions, i la reinterpretació dels resultats obtinguts en termes biològics ha esdevingut una important font de *clarividència*.

Grosso modo, el que ha estat la meva/nostra feina com a *biomatemàtic* durant aquests últims anys es podria resumir de la següent manera.

Generalment, la modelització d'un "fenomen real" no és una tasca fàcil. El punt de partida és la descripció del procés físic, químic o biològic subjacent, en la forma d'un *sistema dinàmic* en

¹Un altre canvi de variables possible és $x = N^{-\theta}$, que transforma l'equació en una de lineal.

un espai de Banach (de dimensió infinita), és a dir, els estats del sistema evolucionen en el temps d'acord amb una certa llei determinista. És ben conegut que els sistemes dinàmics es classifiquen en discrets o continus, segons el conjunt de valors que pren la variable independent temps: \mathbb{Z} o \mathbb{R} . En aquest treball considerarem el temps continu i només per a valors no negatius (*del present al futur*), donant lloc als anomenats sistemes irreversibles. Per a cada temps $t \geq 0$, la solució d'aquest tipus de sistemes es pot veure com a un cert operador en un espai de Banach que associa una condició inicial a la solució del sistema a temps t . Aquest últim és precisament el punt de vista de la teoria de semigrups d'operadors. Vegeu e.g. G.F. Webb en [67]. Vegeu també [64] i [62].

Així doncs ens restringim a models continus, i a models deterministes, en tant que oposats als estocàstics, els quals negligeixen la influència d'esdeveniments aleatoris. No obstant això, els models podran incloure una certa aleatorietat o estocasticitat, per exemple amb la consideració d'una variable aleatòria com a ingredient del model (vegeu el Capítol 2).

Si no està donat ja, un teorema 'ad hoc' d'existència i unicitat de solucions ha de ser establert quan s'estudien sistemes dinàmics continus en dimensió infinita, e.g. equacions en derivades parcials, equacions integrals, equacions funcionals, equacions amb retard ... Usualment aquest tipus de teoremes es proven usant un argument de punt fix (*principi de l'aplicació contractiva*), vegeu el Capítol 2.

Un cop garantides l'existència i la unicitat de solució del problema de valor inicial, ens encarem amb el problema de trobar *estats d'equilibri*, i.e. solucions independents del temps. Aquest tipus de solucions són les més simples i tenen una gran importància ja que constitueixen l'*esquelet* de la dinàmica del sistema.

Si hem tingut èxit en trobar-los, podem intentar investigar la seva *estabilitat*, tant local com global. L'anàlisi de l'estabilitat local d'una solució d'equilibri significa investigar el comportament de les solucions que estan inicialment properes a l'equilibri. La qüestió important de l'estabilitat dels equilibris pot ser de vegades determinada per mitjà d'una certa funció de Liapunov, encara que normalment s'aconsegueix demostrant que l'anomenada *cota de creixement* d'un semigrup d'operadors lineals associat és negativa, a més de demostrar un *principi d'estabilitat lineal* adequat pel al sistema en consideració. El primer fet està relacionat amb la *cota espectral*, i.e. el suprem de les parts reals de l'espectre del generador infinitesimal (vegeu [62] i [74]). El segon fet significa que hem establir una relació entre l'estabilitat del estats d'equilibri i l'estabilitat del sistema linealitzat (vegeu la Secció 3.4.2 i l'Apèndix A). De fet, en la literatura podem trobar principis d'estabilitat lineal per a algunes equacions d'evolució no lineals abstractes, especialment per al cas d'equacions semilineals. Vegeu [68] i [55].

Molt sovint, l'espectre d'un operador lineal (i.e. els valors propis o l'espectre puntual, l'espectre continu, i l'espectre residual, vegeu e.g. [62]) és difícil de calcular. No obstant això, en l'anàlisi de l'estabilitat d'alguns sistemes particulars (algunes equacions d'evolució no lineals governades per operadors *acretius* en espais de Banach), es pot evitar el càlcul de l'espectre si es demostra l'*acretivitat* d'un cert operador lineal. Recordem que la classe dels operadors acretius en espais de Banach (vegeu [11]), que va sorgir com a una extensió de la classe dels operadors monòtons en espais de Hilbert, ve definida per aquells operadors A tals que el seu operador resolvent $J_\lambda := (I + \lambda A)^{-1}$ és una aplicació no expansiva, i.e. $\|J_\lambda y - J_\lambda \bar{y}\| \leq \|y - \bar{y}\|$. Vegeu l'Apèndix A i la Secció 2.7.

A més, es pot estudiar el comportament asimptòtic de les solucions, així com també les bifurcacions dels paràmetres del sistema, i.e. canvis en l'evolució del sistema quan varien els valors dels paràmetres. Per exemple, vegeu el Capítol 3 on provem l'aparició d'un cicle límit (òrbita periòdica isolada) al voltant d'un equilibri per mitjà d'una bifurcació de Hopf. Per a un teorema de bifurcació de Hopf en un marc abstracte de dimensió infinita vegeu [38].

Des del punt de vista de la modelització, ens centrem en models de dinàmica de poblacions que provenen de l'*ecologia*. Més concretament, en el Capítol 2 estudiem un model general per a la dinàmica d'una espècie hermafrodita seqüencial, vegeu la Figura 2.1, i en el Capítol 3 (vegeu [20]) estudiem un model per a la fase sexual d'una espècie haplodiploide en concret (monogonont rotífers, vegeu la Figura 3.1). Ambdós són models (no lineals) continus de poblacions estructurades per l'edat que tenen en compte la reproducció sexual. Altres camps relacionats com poden ser l'epidemiologia, la medicina i la demografia també porten a models de poblacions matemàticament similars. Per a una monografia sobre dinàmica de poblacions estructurades per l'edat vegeu [31], [53] i [74].

Un dels objectius de la dinàmica de poblacions es l'estudi d'alguns aspectes de l'*evolució biològica* per mitjà de la selecció natural.

En poques paraules, la teoria de l'evolució de Darwin es podria explicar dient que els organismes produeixen uns descendents que poden variar lleugerament respecte dels seus pares/progenitors, i la *selecció natural*² afavorirà la supervivència d'aquells que presentin unes peculiaritats que els facin més ben adaptats a l'entorn/ambient en què viuen. L'evolució darwiniana és doncs, un procés amb dues etapes: la variació aleatòria com a matèria primera del procés, i la selecció natural com a força directora. Vegeu [35]. Actualment, l'evolució biològica es defineix de la següent manera: evolució, en el sentit més ampli de la paraula, és senzillament canvi, i per tant

²El concepte de selecció natural va ser desenvolupat de manera independent per dos científics, C.R. Darwin (1809-1882) i A.R. Wallace (1823-1913).

és omnipresent. Les galàxies, les poblacions d'éssers vius, els llenguatges, els sistemes polítics ... tot és susceptible d'evolucionar/canviar/adaptar-se. Més concretament, quan parlem d'evolució biològica parlem de canvis en les característiques hereditàries de les poblacions d'organismes que transcendeixen la durada de la vida d'un sol individu. Cal fer notar que els trets de les poblacions que són considerats com a evolutius són els hereditaris, és a dir, aquells trets que són heretables d'una generació a la següent a través del material genètic. L'evolució biològica comprèn des de petits canvis en la proporció dels diferents al·lels en una mateixa població, fins a les successives alteracions que han tingut lloc des del més primitiu protoorganisme fins als cargols, a les abelles, a les girafes i a les dents de lleó (*taraxacum officinale*).

Ja que alguns dels paràmetres que apareixen en els models ecològics es corresponen amb trets hereditaris de l'espècie en consideració, l'evolució biològica pot ser incorporada en els models definint una certa dinàmica en l'espai de paràmetres (o un subconjunt de). Això últim s'anomena *dinàmica evolutiva* o *dinàmica adaptativa* (vegeu e.g. O. Diekmann en [67]) i és, en la majoria dels casos, una espècie de substitució seqüencial de valors de les característiques vitals de la població, més que un sistema dinàmic pròpiament dit. Es podria dir que la dinàmica adaptativa és una manera de descriure com evolucionen aquests paràmetres, per l'acció combinada de la *mutació aleatòria* i la *selecció natural*. A més, assumint una certa separació d'escala de temps, la dinàmica ecològica (població—escala de temps curta) i la dinàmica evolutiva (tret—escala de temps llarga) poden ser desacoblades l'una de l'altra.

La teoria moderna de la dinàmica adaptativa sorgeix de la teoria de jocs, vegeu e.g. [16] secció 4.9. Originalment desenvolupada per J. von Neumann i O. Morgenstern el 1944, vegeu [73], la teoria de jocs és un model matemàtic usat per estudiar els resultats de les possibles interaccions entre *col·laboradors* i *enemics* en situacions on ningú pot predir completament les accions dels altres, però en canvi, poden adaptar el seu comportament d'acord amb el que “veuen” que els altres fan. J. Maynard-Smith, un dels biòlegs evolutius més cèlebres i influents, va aplicar la teoria de jocs a interaccions entre individus d'una sola espècie que estan en competència entre ells i que usen diferents estratègies per a la seva supervivència.

J. Maynard-Smith va publicar el 1982 el llibre titulat “Evolution and the Theory of Games” [58], on descriu el concepte d'*estratègia evolutivament estable* (ESS). *Grosso modo*, podríem dir que una ESS és una ‘situació de col·laboració estable’, una estratègia que, si és adoptada per la immensa majoria dels individus d'una població, resistirà la invasió per part d'individus amb una nova (diferent) estratègia de supervivència. En el nostre estudi, el criteri decisiu per a l'èxit o fracàs d'una població invasora/mutant és la seva taxa de propagació en les condicions ambientals fixades per l'actual població establerta (també anomenada població resident). Vegeu per exemple

l'article [45].

Per altra banda, Maynard-Smith també és conegut pel seu treball sobre el valor adaptatiu de la reproducció sexual, i per haver provat el doble cost del sexe, l'anomenat cost dels mascles. Aquesta teoria suggereix que si un individu asexual fos introduït en una població d'individus amb reproducció sexual, aviat la reproducció asexual esdevindria la forma predominant. De manera informal, el seu argument es pot explicar de la següent manera. En una població amb reproducció sexual es necessiten dos individus (femella i mascle) per a produir un nou individu. En canvi, una sola femella capaç de reproduir-se partenogenèticament pot produir tants individus com els que poden produir qualsevol parella d'individus reproduint-se sexualment. La subpoblació asexual creixeria, doncs, el doble de ràpida que la subpoblació sexual.

Recentment, nosaltres i altres autors, vegeu e.g. [25], hem estudiat la dinàmica adaptativa per a paràmetres de dimensió infinita, és a dir, hem considerat trets evolutius que són funcions (e.g. la funció de distribució de probabilitat d'un cert procés de transició, vegeu el Capítol 2). Per al càlcul d'estratègies evolutivament estables de trets/característiques de dimensió infinita hem usat el fet que el màxim d'un funcional afí/lineal continu sobre un conjunt compacte i convex, s'assoleix en un punt extrem (o extremal) del conjunt. Per tant el problema té dimensió infinita per dos motius: les variables d'estat pertanyen a un espai funcional, i els paràmetres considerats són funcions.

Finalment, deixeu-nos remarcar de nou que hem estat considerant espècies amb reproducció sexual. La reproducció sexual, típicament definida com la reproducció que involucra la fusió dels *genomes*, és explícitament considerada en tots els models investigats. Aquesta característica ens porta a analitzar des del punt de vista evolutiu, la proporció entre el nombre de femelles i mascles, l'anomenada *sex-ratio* de la població. Aquesta qüestió va ser ja abordada per R.A. Fisher el 1930 (vegeu [42], [32] i [31]), pronosticant una igual proporció de sexes (1 : 1) sota certes hipòtesis simples. De forma resumida, l'argument de Fisher es pot explicar de la següent manera: si hi hagués més individus d'un sexe, en la següent generació seria més adaptatiu produir individus de l'altre sexe ja que aquests tindrien millors condicions per a reproduir-se, equilibrant de nou la proporció entre sexes en la població. Respecte al model d'hermafroditisme seqüencial estudiat en el Capítol 2, també hem trobat una situació senzilla en la qual la població es manté evolutivament en una igual proporció de femelles i mascles, malgrat que això no es compleix per al cas general. El cas en què la fertilitat i la mortalitat són independents de l'edat, on hem provat que els individus canvien de sexe quan assoleixen el 69.3% del seu temps esperat de vida, és un exemple de tal situació.

Resumint, aquesta tesi versa sobre algunes equacions d'evolució, en espais de Banach de di-

mensió infinita, que modelitzen la dinàmica de poblacions estructurades amb reproducció sexual, donant una èmfasi especial en l'evolució biològica conduïda per la selecció natural (dinàmica adaptativa).

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