Mathematical Models and Methods in Applied Sciences

EQUILIBRIUM OF TWO POPULATIONS SUBJECTED TO CHEMOTAXIS

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We consider a system of four partial differential equations modelling the dynamics of two populations interacting via chemical agents. Classes of non-trivial equilibrium solutions are studied and a rescaled total biomass is shown to play the role of a bifurcation parameter.

Keywords: Chemotaxis,bifurcation

1. Introduction

Among all forms of chemosensitivity in which the motion of living cells in organisms is regulated by chemical agents, chemotaxis appears to have particular relevance in many branches of biology. The phenomenon, i.e. the movement of living cells or organisms under the influence of the concentration gradient of a chemical substance - often secreted by the cells or organisms themselves - is considered to be a key factor in morphogenesis, in regulating life cycles of some protozoa, in angiogenesis and vascularization of solid tumors, in seasonal migration of some animal species and so on.

The attempt to study and simulate this phenomenon by means of a mathematical model dates back to 1970, when E.F.Keller and L.A.Segel [17] proposed a model describing displacement and mass conservation for the density $A(\underline{x},t)$ of the living species and for the concentration $P(\underline{x},t)$ of the chemical substance:

$$\frac{\partial A}{\partial t} = \mathrm{div}\,\left(D^A \nabla A - \alpha A \nabla P\right), \tag{1.1}$$

$$\frac{\partial P}{\partial t} = \chi A - \delta P + \mathrm{div}\,\left(D^P \nabla P\right). \tag{1.2}$$

In (1.1) it is assumed that the flux induced by chemotaxis is proportional to $A(\underline{x},t)$ and to the gradient of the concentration of the chemoattractant. Concerning the evolution of $P(\underline{x},t)$, the model postulates a production rate proportional to A and a linear decay of P itself. Of course, the terms containing D^A and D^P in (1.1) and (1.2) represent linear diffusion. The coefficients $\alpha,\ \chi,\ \delta$ are positive constants, although more general situations where also considered including nonlinear diffusivity and chemotactic sensitivity.

Equations (1.1) and (1.2) are supplemented with zero flux boundary conditions and with suitable initial conditions.

The model has been studied extensively, especially in the last decade. For a comprehensive review of the literature the reader is referred to [14]. We confine ourselves to recalling that the well-posedness of the mathematical problem and qualitative properties of the solutions have been investigated also in nonlinear cases (see e.g. [1],[2],[5],[20],[28],[31],[33] as well as [22],[18]). A relevant feature of (1.1)-(1.2) that attracted the attention of many researchers is the possible occurrence of blow-up of solutions for space dimensions $n \geq 2$. This was suggested by [3], following [21], and proved by [16] for $n = 2$, provided that the initial mass $\int_\Omega A\,dx$ exceeds a threshold value, whereas (see also [19]) global existence is granted under mild assumptions if the initial mass is small enough, as well as in one space dimension without any limitation on the initial mass.

In [8] (see also e.g. [10] and [13]) it was shown that the problem admits a radial symmetric solution blowing up at $t = T$ and ehaving like a δ function in $z = 0$, a feature corresponding to the so-called chemotactical collapse i.e. to the situation in which a finite biomass concentrates in a single point.

Actually the meaning of this feature of the model is that chemotaxis can trigger a crucial modification in the biological behaviour of a population that can be identified with a steep-change self-organization mechanisms.

There are cases in which it is preferable to prevent the mathematical model from exhibiting blow-up. To this end the concept of "maximum packing" has been introduced ([11], [23], [24]).

Nonsymmetric blow-up was treated in [12], [15], [30] and symmetrization techniques where used in [4].

Additional interesting properties emerge from the analysis of steady state solutions and of their stability. Already in [17] the stability of the constant solutions of (1.1), (1.2), $A = A_0$, $P = P_0 = \chi A_0/\delta$, was studied in the one-dimensional case. It was shown that a constant solution is linearly stable if the total mass M of the population does not exceed a critical value $\tilde{M}$, depending on the coefficients of the equation and on the width of the slab hosting the population.*

Essentially M is a bifurcation parameter and, as it increases, the system admits more and more non-constant stationary solutions of decreasing wavelength $L/2\pi n$. A fundamental paper on this subject is [25] (see also [25], [32], [29]) where the study of stationary solutions of a general class of Keller-Segel models (possibly including nonlinear diffusivity and chemotactical sensitivity) is reduced to the analysis of a scalar equation $v'' + f(v, \lambda) = 0$.

In the present paper we will deal with a model in which two living populations of densities $A(\underline{x}, t)$ and $B(\underline{x}, t)$ are present in the same domain; we assume that each of them produces a chemical substance, whose concentrations will be denoted by $P(\underline{x}, t)$ and $Q(\underline{x}, t)$, respectively. The rates of production will be proportional to A and B, respectively, through constants χ^P and χ^Q and linear decay will be assumed with constants δ^P and δ^Q.

We assume that P†attracts A and repels B, while Q acts in the opposite way.

Our analysis will be confined to the equilibrium solutions in the one-dimensional case and with some simplifying assumptions on the coefficients with the aim of pointing out some features which are peculiar to two species systems. In particular we will identify a bifurcation parameter, producing periodic solutions of increasing wave number. Numerical examples will be presented.

A very general problem has been considered in a recent paper [34] where an arbitrary number of populations and chemical substances (called sensitivity agents) is evolving in $\mathbb{R}^2$. The conflict-free case is analyzed in detail, conditions of global existence of solutions are discussed, and the possibility of existence of time periodic

*The result is easily extended to more general cases. Moreover analysis of nonlinear instability and its link with occurrence of blow-up is also possible ([6],[29])

†To save notation we use the symbols A, B, P, Q to denote populations and chemicals as well as their concentrations.

attractors is investigated. The main tool is a variational approach, based on the definition of a free energy functional. The equilibria are thus found as the critical points of such functional. The same method could be applied also to our case (some changes are however necessary to take into account that we have to deal with Neumann boundary conditions for the chemical agents); however rather than focusing on general existence results, we are interested here on the characterization of the non-trivial stationary solutions, their multiplicity, their periodicity in space (connected to pattern formation) and so on. In order to obtain this information the simplified form of the model was crucial to derive the detailed estimates we needed.

2. Basic equations

The system occupies the slab $0 < X < L$. According to the discussion of the previous section, the specific currents of the two populations have the form

$$j_A = -D^A \frac{\partial A}{\partial X} + \alpha^A A \frac{\partial P}{\partial X} - \beta^A A \frac{\partial Q}{\partial X}, \tag{2.1}$$

$$j_B = -D^B \frac{\partial B}{\partial X} + \alpha^B B \frac{\partial Q}{\partial X} - \beta^B B \frac{\partial P}{\partial X}. \tag{2.2}$$

Assuming that there is no flux across the boundaries $X = 0,\ X = L$, any stationary solution of the problem must satisfy $j_A = j_B = 0$. On the other hand, the concentrations P and Q at equilibrium will be such that

$$D^P \frac{\partial^2 P}{\partial X^2} + \chi^P A - \delta^P P = 0 \tag{2.3}$$

$$D^Q \frac{\partial^2 Q}{\partial X^2} + \chi^Q B - \delta^Q Q = 0 \tag{2.4}$$

with $\frac{\partial P}{\partial X}$ and $\frac{\partial Q}{\partial X}$ vanishing on $X = 0$ and $X = L$.

Let us now perform the rescaling $x = \frac{X}{L}$, $a = \frac{A}{\hat{a}}$, $b = \frac{B}{\hat{b}}$, $p = \frac{P}{\hat{p}}$, $q = \frac{Q}{\hat{q}}$, with constants $\hat{a}$, $\hat{b}$, $\hat{p}$ and $\hat{q}$ to be selected later.

Denoting by prime the differentiation with respect to x, we have

$$a' + a\left(-\frac{\alpha^A \hat{p}}{D^A} p' + \frac{\beta^A \hat{q}}{D^A} q'\right) = 0, \tag{2.5}$$

$$b' + b\left(-\frac{\alpha^B \hat{q}}{D^B} q' + \frac{\beta^B \hat{p}}{D^B} p'\right) = 0, \tag{2.6}$$

$$p'' + \frac{\chi^P L^2}{D^P} \frac{\hat{a}}{\hat{p}} a - \frac{\delta^P L^2}{D^P} p = 0, \tag{2.7}$$

$$q'' + \frac{\chi^Q L^2}{D^Q} \frac{\hat{b}}{\hat{q}} b - \frac{\delta^Q L^2}{D^Q} q = 0. \tag{2.8}$$

We impose a first simplifying assumption, namely

$$\alpha^A \alpha^B = \beta^A \beta^B. \tag{2.9}$$

Although the motivation of (2.9) is rather of technical nature, it is worth to outline that the ratios α^A/β^A and β^B/α^A measure the relative sensitivity (of each of the two species) to chemical agents P and Q. Thus, (2.9) means that the relative effectiveness of the two chemicals on the two species is the same.

Note also that, in case of vanishing diffusivities, (2.9) is a necessary condition for the existence of non-constant stationary solutions.

Then, choosing

$$\hat{p} = \frac{D^A}{\alpha^A}, \quad \hat{q} = \frac{D^A}{\beta^A}, \tag{2.10}$$

(2.5) and (2.6) become

$$a' + a\,(-p' + q') = 0, \tag{2.11}$$
$$b' + b\lambda\,(-q' + p') = 0, \tag{2.12}$$

where

$$\lambda = \frac{\alpha^B}{\beta^A}\frac{D^A}{D^B}\left(= \frac{\beta^B}{\alpha^A}\frac{D^A}{D^B}\right). \tag{2.13}$$

At this point (2.7), (2.8) suggest a natural choice of the remaining quantities $\hat{a}$ and $\hat{b}$ i.e.

$$\hat{a} = \frac{D^P D^A}{\alpha^A}\frac{1}{\chi^P L^2}, \tag{2.14}$$
$$\hat{b} = \frac{D^Q D^A}{\beta^A}\frac{1}{\chi^Q L^2}. \tag{2.15}$$

Hence

$$p'' + a - \mu_P^2 p = 0, \quad p'(0) = p'(1) = 0 \tag{2.16}$$
$$q'' + b - \mu_Q^2 q = 0, \quad q'(0) = q'(1) = 0 \tag{2.17}$$

where

$$\mu_P^2 = \frac{\delta^P}{D^P}L^2, \quad \mu_Q^2 = \frac{\delta^Q}{D^Q}L^2. \tag{2.18}$$

Subtracting (2.17) from (2.16) we obtain a differential equation for the function

$$\eta(x) = p(x) - q(x), \tag{2.19}$$

provided that

$$\frac{\delta^P}{D^P} = \frac{\delta^Q}{D^Q}, \tag{2.20}$$

so that $\mu_P^2 = \mu_Q^2 = \mu^2$. The latter condition and (2.9) are physical limitations. Nevertheless, as we shall see, the resulting system possesses a rather rich and interesting set of solutions.

The differential equation for η is

$$\eta'' + a - b - \mu^2\eta = 0. \tag{2.21}$$

Of course, (2.11), (2.12) imply

$$a(x) = Ce^{\eta(x)}, \tag{2.22}$$
$$b(x) = De^{-\lambda\eta(x)}, \tag{2.23}$$

where C and D are positive integration constants. Then, any solution to our problem will satisfy, for some positive C and D, the boundary value problem

$$\begin{cases} \eta''(x) + Ce^{\eta(x)} - De^{-\lambda\eta(x)} - \mu^2\eta(x) = 0, \ 0 < x < 1 \\ \eta'(0) = \eta'(1) = 0 \end{cases} \tag{2.24}$$

Conversely if (2.24) admits a solution $\eta(x)$ for some positive constants C and D, then a solution (a, b, p, q) to the original problem is provided. Indeed, a and b are given by (2.22) and (2.23) and p is found by solving the following problem

$$p'' - \mu^2 p = -Ce^{\eta}, \quad p'(0) = p'(1) = 0. \tag{2.25}$$

The linear differential equation is easily integrated by the classical method of Lagrange, finding the general solution

$$p(x) = [\gamma_1 + c_1(x)]\, e^{\mu x} + [\gamma_2 + c_2(x)]\, e^{-\mu x}, \tag{2.26}$$

where

$$c_1(x) = -\frac{C}{2\mu}\int_0^x e^{\eta(\xi)-\mu\xi}\, d\xi, \tag{2.27}$$

$$c_2(x) = \frac{C}{2\mu}\int_0^x e^{\eta(\xi)+\mu\xi}\, d\xi. \tag{2.28}$$

Then imposing the boundary conditions yields

$$\gamma_1 = \gamma_2 = \frac{c_2(1)e^{-\mu} - c_1(1)e^{\mu}}{e^{\mu} - e^{-\mu}} := \gamma. \tag{2.29}$$

Proposition 2.1. *For any $\eta(x)$ solving (2.24), $p(x)$ defined by (2.26) is positive.*

Indeed, $p(0) = 2\gamma$ is positive by (2.29), (2.27), (2.28). Moreover, if a first $\bar{x} \in (0, 1]$ exists such that $p(\bar{x}) = 0$, i.e.

$$(\gamma + c_1(\bar{x}))e^{\mu\bar{x}} + (\gamma + c_2(\bar{x}))e^{-\mu\bar{x}} = 0$$

since

$$\frac{p'(\bar{x})}{\mu} = (\gamma + c_1(\bar{x}))e^{\mu\bar{x}} - (\gamma + c_2(\bar{x}))e^{-\mu\bar{x}}$$

(note that $c_1' e^{\mu x} + c_2' e^{-\mu x} = 0$), the sign of $p'(\bar{x})$ is the sign of $\gamma + c_1(\bar{x})$. But

$$\gamma + c_1(\bar{x}) > \gamma + c_1(1) = \frac{e^{-\mu}}{e^{\mu} - e^{-\mu}}(c_2(1) - c_1(1)) > 0.$$

Thus, a contradiction is found.□

Similarly $q(x)$ is the solution of

$$q'' - \mu^2 q = -De^{-\lambda\eta(x)}$$

(or simply $q = p - \eta$) and is positive by the same argument of Remark 2.1.

3. Finding nontrivial solutions

We have seen that, in our assumptions, solving (2.24) is equivalent to finding a quadruple (a, b, p, q) satisfying (2.11), (2.12), (2.16), (2.17) (with $\mu_P^2 = \mu_Q^2$).

Of course (2.24) admits the trivial solutions $\eta = \eta_0$ such that $Ce^{\eta_0} - De^{-\lambda\eta_0} - \mu^2\eta_0 = 0$. In particular, $\eta_0 = 0$ is a solution for any $C = D$. This corresponds to $a = b = M$ and $p = q = \frac{M}{\mu^2}$. We are interested in non-trivial solutions of the boundary value problem (2.24).

General bifurcation results were obtained in [25],[26] for the boundary value problem

$$v'' + f(v, c) = 0, \quad v'(0) = v'(1) = 0 \tag{3.1}$$

where c is a parameter in $\mathbb{R}^n$ (see also the already quoted papers [29],[32]). The elegant argument developed there allows to select general classes of functions $f(v, c)$ for which (in particular) equilibrium can be successfully studied, but, conversely, provides less information when cases of different nature are dealt with.[‡] We will follow essentially the same strategy considered in the study of the "time map" of a nonlinear oscillator, but will obtain the relevant advantage of relating the bifurcation parameter to an appropriately rescaled mass of the two species.

Problem (2.24) can be interpreted as a problem for a nonlinear oscillator with potential energy

$$V(\eta) = -\frac{1}{2}\mu^2\eta^2 + Ce^{\eta} + \frac{D}{\lambda}e^{-\lambda\eta} \tag{3.2}$$

with $C > 0$, $D > 0$. Our aim is to find a solution $\eta(x)$ that have period $\frac{2}{k}$ with k integer.

It is immediately seen that $V(\eta) \to +\infty$ as $\eta \to \pm\infty$ and that V'' is a convex function. Therefore, only two cases can occur:

A. V has two minima $V^{(1)}_{min}$, $V^{(2)}_{min}$ and one maximum V_{max},

B. V has just one minimum.

Case **B** includes limit situations (on the borderline with case **A**), namely

$\mathbf{B_1}$ V' vanishes in one more point, distinct from the minimum, where $V'' = 0$, $V''' \neq 0$; in the minimum $V^{(IV)} > 0$,

$\mathbf{B_2}$ $V' = V'' = V''' = 0$ at the minimum, where $V^{(IV)} > 0$.

We may pass from **A** to **B** either through $\mathbf{B_1}$ (the maximum tends to one of the minima) or through $\mathbf{B_2}$ (the maximum and the two minima tend to coalesce).

In correspondence to the extrema of V we find the constant solutions. The problem of finding nontrivial solutions to (2.11) (2.12) (2.16) (2.17) is equivalent to:

Problem 3.1. *Find C and D so that problem (2.24) has nonconstant solutions, i.e. so that the nonlinear oscillator with potential energy (3.2) has solutions with half-period $\frac{1}{k}$, $k \in \mathbb{N}$.*

We introduce the following classification of nontrivial solutions of (2.24).

Definition 3.1. *The increasing branch of an oscillation of semiperiod* 1 *is a solution of* class 1 *of problem 3.1. In a similar way we define class k solutions.*

Of course, if $\eta(x)$ is a class 1 solution, $\eta(1 - x)$ is also a solution of (2.24), with $\eta'(x) < 0$ and $\eta(0) > \eta(1)$. The same transformation generates solutions from class k solutions.

[‡]For istance the assumptions of the basic Theorem 3.3 of [26] are not necessarily satisfied in our problem.

It is easy to realize that there are no other solutions.

For any $C, D > 0$ and μ^2 given, we consider the problem:

$$\eta'' + V'(C, D, \eta) = 0, \tag{3.3}$$

$$\eta(0) = \eta_0, \quad \eta'(0) = 0, \tag{3.4}$$

with

$$V(C, D, \eta) = -\frac{1}{2}\mu^2\eta^2 + Ce^{\eta} + \frac{D}{\lambda}e^{-\lambda\eta}. \tag{3.5}$$

We define $E = V(C, D, \eta_0)$ as the energy of the nonlinear oscillator. So η_0 and η_1 are "conjugate resting points" corresponding to the selected energy E. We may suppose $\eta_0 < \eta_1$. The semiperiod of the oscillation can be expressed as a function of E as follows:

$$T(E) = \frac{1}{\sqrt{2E}} \int_{\eta_0(E)}^{\eta_1(E)} \left(1 - \frac{V}{E}\right)^{-\frac{1}{2}} d\eta. \tag{3.6}$$

A simple analysis of function V leads immediately to the determination of sufficient conditions for the existence of nontrivial solutions. To this purpose we remark that if E approaches a value corresponding to a maximum or a horizontal inflection point of V, then $T(E) \to +\infty$. Another basic feature of $T(E)$ is preoved in

Proposition 3.1. *We have*

$$\lim_{E\to\infty} T(E) = 0. \tag{3.7}$$

Proof. When E grows to $+\infty$ we may approximate η_0, η_1 as follows

$$\eta_0(E) \simeq \frac{1}{\lambda}\log\frac{D}{\lambda E}, \tag{3.8}$$

$$\eta_1(E) \simeq \log\frac{E}{C}, \tag{3.9}$$

so that

$$\eta_1(E) - \eta_0(E) \simeq \log\frac{\lambda^{\frac{1}{\lambda}} E^{1+\frac{1}{\lambda}}}{CD^{\frac{1}{\lambda}}}. \tag{3.10}$$

After the usual substitution $\eta = \eta_0 + (\eta_1 - \eta_0)y$, (3.6) yields

$$T = \frac{\eta_1 - \eta_0}{\sqrt{2E}} \int_0^1 \frac{dy}{\sqrt{1 - \frac{V}{E}}}. \tag{3.11}$$

Letting E go to $+\infty$, the ratio $\frac{V}{E}$ tends to zero uniformly in any interval $(\varepsilon, 1-\varepsilon)$, ε being a fixed positive arbitrarily small number.

Since the factor $\frac{\eta_1-\eta_0}{\sqrt{E}}$ tends to zero as $(1+\frac{1}{\lambda})E^{-\frac{1}{2}}\log E$, we only have to study the integrals in $(0, \varepsilon)$ and in $(1-\varepsilon, 1)$.

For $y \in (1-\varepsilon, 1)$ the dominating term in $\frac{V}{E}$ is

$$\frac{V}{E} \simeq \frac{C}{E}e^{\eta_0 + (\eta_1 - \eta_0)y} \simeq \left[\frac{\lambda C D^{\frac{1}{\lambda}}}{(\lambda E)^{1+\frac{1}{\lambda}}}\right]^{1-y}. \tag{3.12}$$

Putting

$$Z = \frac{\lambda C D^{\frac{1}{\lambda}}}{(\lambda E)^{1+\frac{1}{\lambda}}} < 1, \tag{3.13}$$

we have to calculate

$$\int_{1-\varepsilon}^{1} \left(1 - Z^{1-y}\right)^{-\frac{1}{2}} dy = \int_{0}^{\varepsilon} (1 - Z^{z})^{-\frac{1}{2}} dz \tag{3.14}$$

Introducing $\zeta = Z^z$ we write the same integral as

$$\frac{1}{|\log Z|} \int_{Z^{\varepsilon}}^{1} (1-\zeta)^{-\frac{1}{2}} \zeta^{-1}\, d\zeta = \tag{3.15}$$

$$\frac{2}{|\log Z|} \int_0^{\sqrt{1-Z^{\varepsilon}}} \frac{dY}{1-Y^2} = \frac{1}{|\log Z|} \log \frac{1+\sqrt{1-Z^{\varepsilon}}}{1-\sqrt{1-Z^{\varepsilon}}}.$$

For $E >> 1$ i.e. $Z << 1$ it behaves like $\frac{|logZ^{\varepsilon}|}{|logZ|} = \varepsilon$.

A similar conclusion holds for the integral on $(0, \varepsilon)$.

Thus it is confirmed that

$$T(C, D, E) \simeq \frac{1}{\sqrt{2}}(1 + \frac{1}{\lambda})E^{-\frac{1}{2}} \log E \tag{3.16}$$

for $E >> 1$. □

As a consequence of the above properties we deduce the following

Proposition 3.2. *In case* **A** *consider the two families of oscillations corresponding to energies in the intervals* $(V_{min}^{(1)}, V_{max})$, $(V_{min}^{(2)}, V_{max})$. *Let* $T_{min}^{(1)}$, $T_{min}^{(2)}$ *be the semiperiods of the linearized oscillations near the respective minima. Then if* $T_{min}^{(i)} < 1$ *there are class* k *solutions with energy in* $(V_{min}^{(i)}, V_{max})$ *for all* k *such that* $1/k > T_{min}$. *In addition, there are class* k *solutions for all* $k \in \mathbb{N}$ *with suitable values of* $E > V_{max}$.

Case $\mathbf{B_1}$ *is quite similar, because the horizontal inflection point has the same effect as the maximum (i.e. produces a singularity of* T*).*

In case $\mathbf{B_2}$ *the period tends to* $+\infty$ *when* $E \downarrow V_{min}$ *and therefore the existence of class* k *solution is guaranteed for any* k.

In the remaining situations of case **B** *we can say that there exist solutions of class* k *for all those integers* k *such that* $1/k < T_{min}$, *where* T_{min} *is the semiperiod of the linearized oscillations near the only minimum of* V.

4. Determination of regions in the (C, D) plane in which class k solutions exist.

Our next aim is to characterize the sets of points in the (C, D) plane such that $V''(C, D, \eta)$ has a prescribed value in one of the extremal points for V. These curves have the parametric equations $V'(C, D, \eta) = 0$, $V''(C, D, \eta) = (\theta - 1)\mu^2$, i.e.

$$\begin{cases} Ce^{\eta} - De^{-\lambda\eta} = \mu^2\eta, \\ Ce^{\eta} + \lambda De^{-\lambda\eta} = \mu^2\theta. \end{cases} \tag{4.1}$$

We are primarily interested in nonnegative values of V'' and therefore we start the analysis of (4.1) from the case $\theta \geq 1$.

We have

$$C = \frac{\mu^2}{1+\lambda}(\theta + \lambda\eta)e^{-\eta}, \tag{4.2}$$

$$D = \frac{\mu^2}{1+\lambda}(\theta - \eta)e^{\lambda\eta}. \tag{4.3}$$

Here η is a parameter ranging in the interval $[-\frac{\theta}{\lambda}, \theta]$; note that (4.2), (4.3) define a nonsingular curve for any $\theta > 1$, starting from the D axis in

$$D_{0\,\theta} = \frac{\mu^2\theta}{\lambda}e^{-\theta}, \qquad \eta = -\frac{\theta}{\lambda}, \tag{4.4}$$

intersecting the line $C = D$ ($\eta = 0$) in $\frac{\mu^2}{1+\lambda}\theta$ and reaching the C axis ($\eta = \theta$) in the point

$$C_{0\,\theta} = \mu^2\theta e^{-\theta}. \tag{4.5}$$

For $\theta = 1$, (4.2) and (4.3) define the set of the (C, D) plane where V' and V'' both vanish, a situation encompassing the singular cases B_1 and B_2. In this case the set can be decomposed in two regular curves originating from points $(0, D_{0\,1})$ and $(C_{0\,1}, 0)$ (where $D_{0\,1}$ and $C_{0\,1}$ are obtained putting $\theta = 1$ in (4.4) and (4.5)). On each of the two curves both C and D increase up to the point in which a cusp is formed. The cusp coordinates are

$$C_{m\,1} = \frac{\mu^2\lambda}{1+\lambda}e^{\frac{1-\lambda}{\lambda}}, \tag{4.6}$$

$$D_{m\,1} = \frac{\mu^2}{\lambda(1+\lambda)}e^{\lambda-1}, \tag{4.7}$$

corresponding to the value $\eta = 1 - \frac{1}{\lambda}$, where both (4.2), (4.3) with $\theta = 1$ take their maximum, and lying on the curve

$$C^\lambda D = \left(\frac{\mu^2}{1+\lambda}\right)^{1+\lambda} \lambda^{\lambda-1} \tag{4.8}$$

which expresses the property $\inf_\eta V'' = 0$ (eliminate η between $V'' = 0$, $V''' = 0$ and note that $V^{(IV)} > 0$).

In other words, the two branches of (4.2), (4.3) with $\theta = 1$ correspond to case $\mathbf{B_1}$ and bound (with the axes) the region $\mathcal{A}$ where C and D are such that $V(C, D, \eta)$ has a maximum. The points satisfying (4.6)-(4.7) corresponds to case $\mathbf{B_2}$.

The complementary region $\mathcal{B}$ is divided in three subsets. In the subset lying above the curve (4.8) the function V has only one minimum and no inflection points. In the other two subsets the function V has one minimum and one non-horizontal inflection point (see Figure 4.1).

To complete the study of (4.2) and (4.3) we may note that the maximum $C_{m,\theta}$ of C and the maximum $D_{m,\theta}$ of D on the curve are reached for $\eta = 1 - \frac{\theta}{\lambda}$ and for $\eta = \theta - \frac{1}{\lambda}$,

$$C_{m\,\theta} = C_{m\,1}e^{\frac{\theta-1}{\lambda}} \tag{4.9}$$

$$D_{m\,\theta} = D_{m\,1}e^{\lambda(\theta-1)}. \tag{4.10}$$

Note that $C_{m\,\theta} > C_{m\,1}$, $D_{m\,\theta} > D_{m\,1}$ for $\theta > 1$ (the inequalities are reversed for $\theta < 1$).

Another property of the curves can be pointed out calculating the maximum of the product $C^\lambda D$:

$$C^\lambda D = \left(\frac{\mu^2}{1+\lambda}\right)^{1+\lambda} (\theta + \lambda\eta)^\lambda (\theta - \eta) \tag{4.11}$$

which is taken for $\eta = \frac{\theta(\lambda-1)}{\lambda}$ and is precisely

$$\left(C^\lambda D\right)_{max} = \left(\frac{\mu^2}{1+\lambda}\right)^{1+\lambda} \lambda^{\lambda-1}\theta^\lambda \tag{4.12}$$

Thus for $\theta > 1$ all the curves have an arc lying above the curve (4.8). Indeed they cross region $\mathcal{A}$, the three regions $\mathcal{B}$ and their mutual interfaces, meaning that a minimum with a selected curvature may occur in each of the situations described by the various subsets.

It must be also remarked that for $\theta > 1$ each of the curves (4.2), (4.3) has a point of self-intersection, necessarily in the region $\mathcal{A}$, meaning that the prescribed curvature can be taken in either of the two minima.

In addition each curve carrying a given value of $\theta > 1$ will intersect twice the curves with other values of $\theta > 1$, in the region $\mathcal{A}$. For the sake of completeness we can also observe that the conditions $C > 0$, $D > 0$ require $\theta > 0$ (i.e. V'' cannot be less then $-\mu^2$) and for $\theta \in (0, 1)$ the curves are entirely within the region $\mathcal{A}$ (not shown in Figure 4.2).

We also remark that T is not defined on the axes (one population case) outside the closure of the region $\mathcal{A}$ ($C > \mu^2 e^{-1}$ for $D = 0$, and $D > \mu^2\lambda^{-1}e^{-1}$ for $C = 0$).

The information now available about the family of curves in the quarter plane $C > 0$, $D > 0$ carrying a prescribed curvature at the minimum (or in one of the minima) of $V(C, D, \eta)$ allows us to draw some conclusions concerning the existence of class k solutions. It is enough to recall Proposition 3.2 and the fact that the semiperiod $T^\star$ of the linearized oscillations around a minimum point $\eta^\star$ of V is $T^\star = \pi \left[V''(\eta^\star)\right]^{-\frac{1}{2}}$.

Theorem 4.1. *In the closure of region $\mathcal{B}$ class k solutions exist on the set of curves satisfying*

$$\theta - 1 < \left(\frac{k\pi}{\mu}\right)^2 \tag{4.13}$$

for suitable levels of the "energy" E.

In region $\mathcal{A}$, besides the class k solutions (for all k) that can be found for sufficiently large values of E, there will be at least two more solutions in the subset in which two curves both carrying values of θ such that

$$\theta - 1 > \left(\frac{k\pi}{\mu}\right)^2 \tag{4.14}$$

intersect each other. The existence of at least one more solution is instead guaranteed in the set of the intersections of one curve of type (4.13) and one of type (4.14).

From the analysis made at the end of section 3, it comes out that a particular role is played by the curve carrying the value of V'' at the minimum corresponding

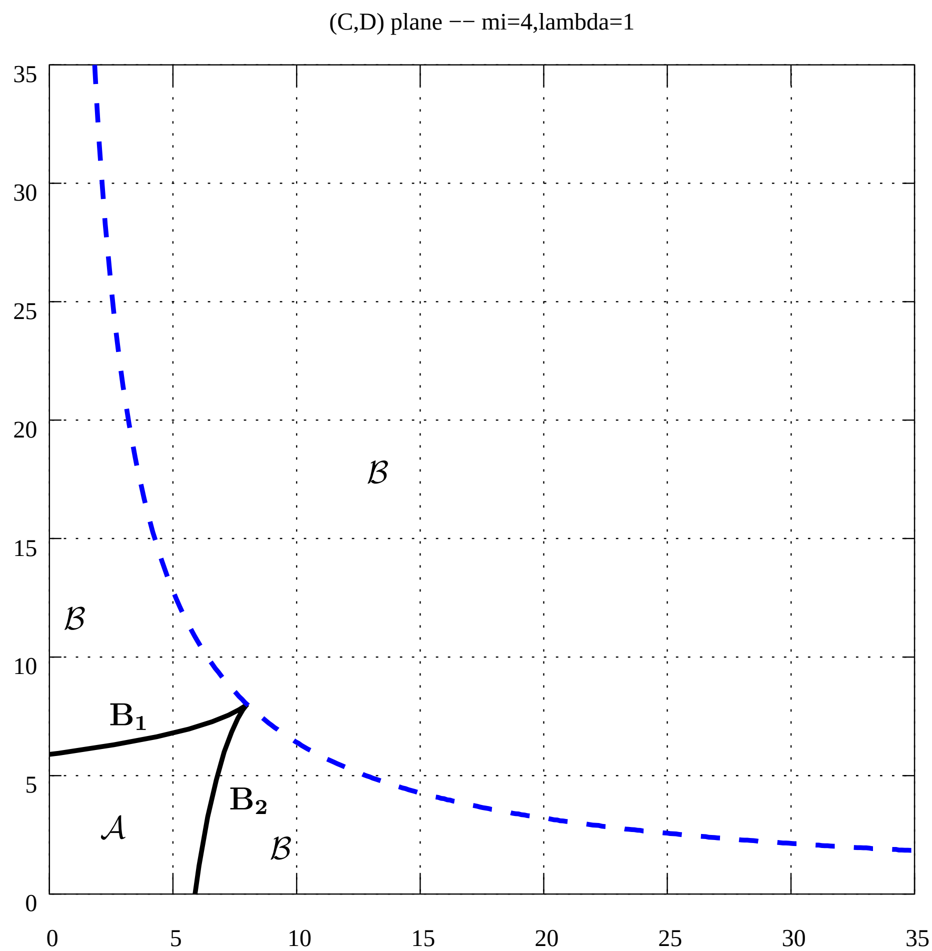


Figure 4.1: In region $\mathcal{A}$ function $V(C, D, \cdot)$ has two minima and one maximum. In region $\mathcal{B}$ there is just one minimum. Region $\mathcal{B}$ is crossed by thecurve defined by $\inf V'' = 0$ (dashed); above this curve $V(C, D, \cdot)$ has not inflection points.

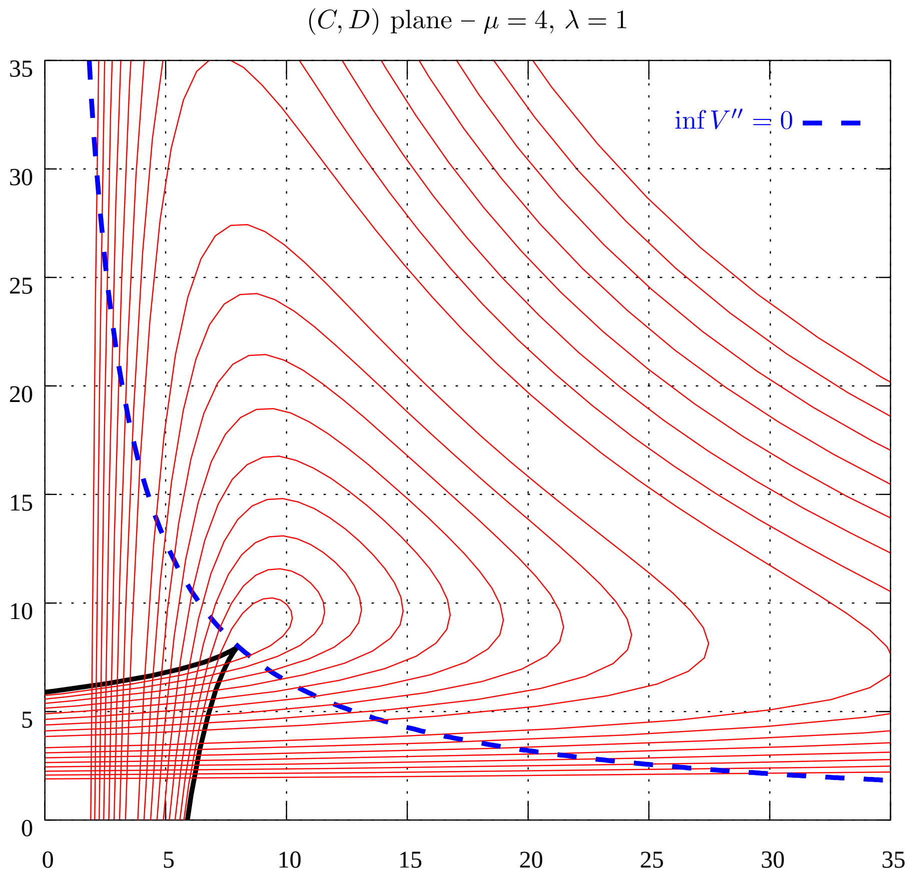


Figure 4.2: Curves defined by $V'' = (1 - \theta)\mu^2,\ V' = 0$ for $\theta \geq 1$.

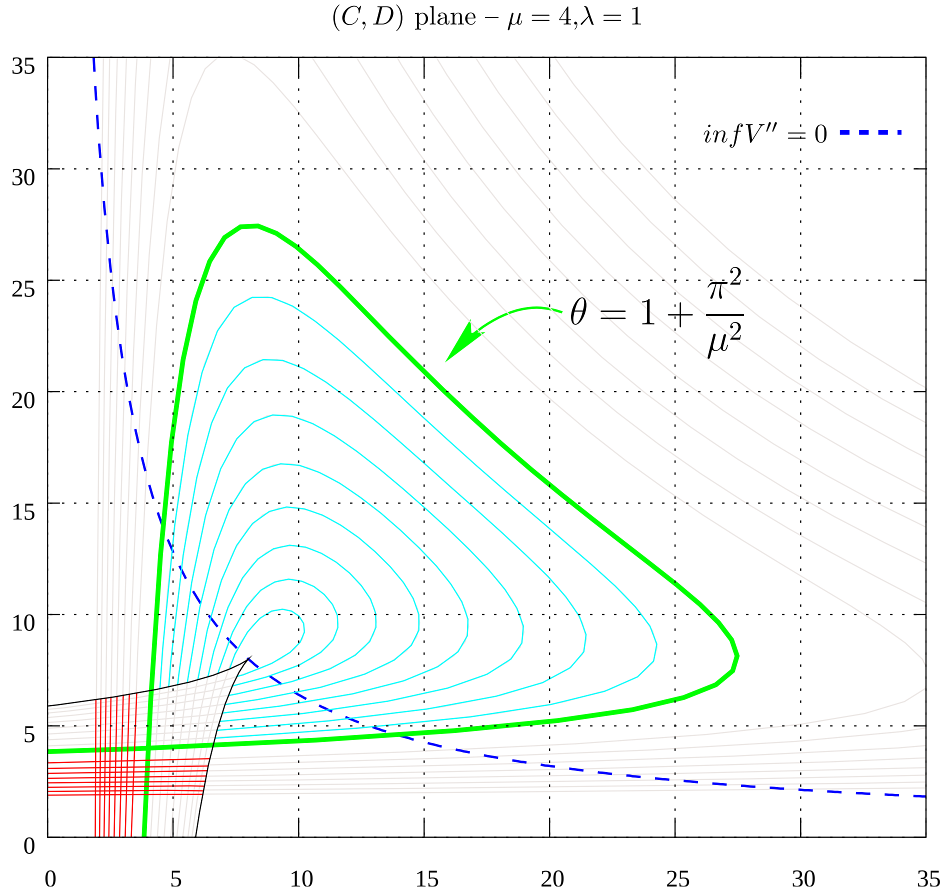


Figure 4.3: Curves of Figure 4.2 satisfying conditions (4.13) and (4.13) for $k = 1$.

to the semiperiod 1 of the small oscillations, i.e. $2\pi^2$. Hence we are interested in the curve labelled by $\theta = \theta_0 = 1 + \frac{2\pi^2}{\mu^2}$, which is a kind of separatrix. For $\theta > \theta_0$ the semiperiod defined above is less than 1, for $\theta < \theta_0$ it is greater than 1.

Thus we arrived at the following conclusions:

Theorem 4.2. *(i) class* 1 *solutions are associated to the subset of the closure of region $\mathcal{A}$ crossed by the curves (4.2), (4.3) with $\theta < \theta_0$*

(ii) class 1 *solutions are associated to the subset of region $\mathcal{B}$ crossed by the curves (4.2), (4.3) with $\theta > \theta_0$.*

However we remark that these conditions are only sufficient for the existence of class 1 solutions, since they are based only on the comparison of asymptotic cases with the small oscillations at minimum and on a continuity argument.

5. Bifurcation thresholds for the total cellular mass

The analysis performed in the previous section provides only a partial answer to the problem, because we only found sufficient conditions for the existence of class k solutions, at least with some multiplicity.

The limit of such analysis is the lack of information on how the semiperiod T depends on E, for fixed C, D. Although it can be seen that $\frac{\partial T}{\partial E}$ is bounded when T is not singular, such a dependence looks too complicated to be investigated thoroughly. However, if we organize the class of functions $V(C, D, \eta)$ according to a different criterion, we can focus our attention on another physically significant question: what is the minimal total (rescaled) cellular mass compatible with the existence of a class k solution ? As a matter of fact, we will prove that this quantity plays the role of a bifurcation parameter.

By total rescaled mass we mean the sum

$$M_{TOT} = M_a + \frac{1}{\lambda} M_b \tag{5.1}$$

where

$$M_a = C \int_0^1 e^{\eta(x)}\, dx, \quad M_b = D \int_0^1 e^{-\lambda\eta(x)}\, dx \tag{5.2}$$

represent the nondimensional masses of the two populations, according to (2.22), (2.23).

The main result of this section is the following

Theorem 5.1. *Class k solutions bifurcate from the set of constant solutions at the following values of the rescaled total mass:*

$$M_k = k^2\pi^2 + \mu^2 \quad \textit{for } \lambda \le 1, \tag{5.3}$$

$$M_k = \frac{k^2\pi^2 + \mu^2}{\lambda^2} \quad \textit{for } \lambda > 1. \tag{5.4}$$

The proof of this theorem requires several intermediate results and will be presented at the end of the section. The first step is the following lemma.

Lemma 5.1. *For any given pair η_0,η_1, $\eta_0 < \eta_1$, there exists $C_0(\eta_0, \eta_1)$ such that for any $C > C_0$, $\exists!\, D > 0$ such that $V(C, D, \eta)$ satisfies*

$$V(C, D, \eta_0) = V(C, D, \eta_1), \tag{5.5}$$

$$V(C, D, \eta) < V(C, D, \eta_0), \quad \eta \in (\eta_0, \eta_1). \tag{5.6}$$

Proof. From now on whenever this is not misleading we simply denote $V(C, D, \eta)$ by $V(\eta)$.

Imposing (5.5) yields

$$\frac{D}{\lambda} = \Gamma(\eta_0, \eta_1) + C\Delta(\eta_0, \eta_1) \tag{5.7}$$

with

$$\Gamma(\eta_0, \eta_1) = \frac{\mu^2}{2} \frac{\eta_1^2 - \eta_0^2}{e^{-\lambda\eta_0} - e^{-\lambda\eta_1}}, \tag{5.8}$$

$$\Delta(\eta_0, \eta_1) = \frac{e^{\eta_1} - e^{\eta_0}}{e^{-\lambda\eta_0} - e^{-\lambda\eta_1}}. \tag{5.9}$$

Both (5.6) and the condition $D > 0$ may require further limitations on C, besides $C > 0$.

Clearly, $D > 0$ is guaranteed by

$$C > -\frac{\Gamma}{\Delta}. \tag{5.10}$$

This condition is absorbed by $C > 0$ when $\Gamma > 0$ (i.e. $\eta_0 < 0$ and $\eta_0 < \eta_1 < -\eta_0$), otherwise it is stronger than $C > 0$.

Inequality (5.6) is equivalent to

$$C\left[\frac{e^{-\lambda\eta} - e^{-\lambda\eta_1}}{e^{-\lambda\eta_0} - e^{-\lambda\eta_1}} - g(\eta)\right] < -\frac{\Gamma}{\Delta}\left[\frac{\eta^2 - \eta_0^2}{\eta_1^2 - \eta_0^2} - g(\eta)\right] \tag{5.11}$$

where

$$g(\eta) = \frac{e^{-\lambda\eta_0} - e^{-\lambda\eta}}{e^{-\lambda\eta_0} - e^{-\lambda\eta_1}}. \tag{5.12}$$

The quantity in square brackets multiplying C in (5.11) is negative in (η_0, η_1), since it vanishes for $\eta = \eta_0, \eta = \eta_1$, and its second derivative is positive. So the l.h.s. in (5.11) is negative for all $C > 0$, while the r.h.s. can assume either sign. Elementary calculations show that the ratio

$$-\Gamma \frac{\left[\frac{\eta^2 - \eta_0^2}{\eta_1^2 - \eta_0^2} - g(\eta)\right]}{\left[\frac{e^{-\lambda\eta} - e^{-\lambda\eta_1}}{e^{-\lambda\eta_0} - e^{-\lambda\eta_1}} - g(\eta)\right]}$$

is bounded and we denote its supremum in (η_0, η_1) by $H(\eta_0, \eta_1)$.

Thus the inequalities $C > 0$, (5.10) and (5.11) are simultaneously fulfilled provided that $C > C_0(\eta_0, \eta_1)$ with

$$C_0(\eta_0, \eta_1) = \frac{1}{\Delta} \max\left\{[-\Gamma]^+, H\right\} \tag{5.13}$$

$[\cdot]^+$ denoting the positive part. Thus the lemma is proved. □

In this way, for each ordered pair (η_0, η_1) we have constructed a one-parameter family of functions satisfying (5.5),(5.6) which we denote simply by $V_c(\eta)$:

$$V_c(\eta) = -\frac{1}{2}\mu^2\eta^2 + Ce^{\eta} + [\Gamma(\eta_0, \eta_1) + C\Delta(\eta_0, \eta_1)]\, e^{-\lambda\eta} \tag{5.14}$$

Now we consider the increasing branch of the oscillation from η_0 to η_1, generated by $V_c(\eta)$, whose semiperiod is

$$T(C,\eta_0,\eta_1) = \frac{1}{\sqrt{2}} \int_{\eta_0}^{\eta_1} \frac{d\eta}{\sqrt{V_c(\eta_0) - V_c(\eta)}}. \tag{5.15}$$

The following lemma points out the advantage of this approach.

Lemma 5.2. *For any $C > C_0(\eta_0,\eta_1)$ T is differentiable with respect to C and*

$$\frac{\partial T}{\partial C} < 0. \tag{5.16}$$

Moreover

$$\lim_{C\to+\infty} T(C,\eta_0,\eta_1) = 0. \tag{5.17}$$

Proof. From (5.14)

$$\frac{\partial V_c(\eta)}{\partial C} = e^{\eta} + \Delta(\eta_0,\eta_1)e^{-\lambda\eta}, \tag{5.18}$$

so that we can write

$$\frac{\partial V_c(\eta_0)}{\partial C} - \frac{\partial V_c(\eta)}{\partial C} = -(e^{\eta_1} - e^{\eta_0}) \left[\frac{e^{\eta} - e^{\eta_0}}{e^{\eta_1} - e^{\eta_0}} - g(\eta) \right]. \tag{5.19}$$

We already know that the factor in square brackets is negative for $\eta \in (\eta_0,\eta_1)$. Moreover, its first derivative takes non-zero values in η_0 and η_1. As a consequence, we may differentiate (5.15):

$$\frac{\partial T}{\partial C} = -\frac{1}{2\sqrt{2}} \int_{\eta_0}^{\eta_1} \left(\frac{\partial V_c(\eta_0)}{\partial C} - \frac{\partial V_c(\eta)}{\partial C} \right) (V_c(\eta_0) - V_c(\eta))^{-\frac{3}{2}}\, d\eta \tag{5.20}$$

(the integral is still convergent), and (5.16) is proved.

In order to prove (5.17) it is enough to remark that $(V_c(\eta_0) - V_c(\eta))^{-\frac{1}{2}}$ tends to zero as $\frac{1}{\sqrt{C}}$ uniformly in each closed interval contained in (η_0,η_1). □

As a corollary, we can say that

$$\bar{T}(\eta_0,\eta_1) = \sup_{C>C_0(\eta_0,\eta_1)} T(C,\eta_0,\eta_1) \tag{5.21}$$

is also the limit of $T(C,\eta_0,\eta_1)$ as $C \downarrow C_0(\eta_0,\eta_1)$. □

Another consequence is that monotonicity provides now a necessary and sufficient condition for existence:

Theorem 5.2. *The condition*

$$\bar{T}(\eta_0,\eta_1) > \frac{1}{k} \tag{5.22}$$

is necessary and sufficient for the existence of precisely one class k solution characterized by the extreme values η_0, η_1.

Suppose now that (5.22) is satisfied for some $k \in \mathbb{N}$, with η_0, η_1 given. We know that there exists one and only one $C_k(\eta_0, \eta_1) > C_0(\eta_0, \eta_1)$ and correspondingly one and only one $D_k(\eta_0, \eta_1) > 0$, such that the potential V_{c_k} produces an oscillation between η_0 and η_1 with semiperiod $\frac{1}{k}$.
We want to study the dependence of C_k and D_k on η_1.

Lemma 5.3. *Suppose (5.22) is fulfilled for $\eta_1 \in (\eta_0, \eta_0 + \zeta)$ for some $\zeta > 0$ and η_0 given. Then the functions $C_k(\eta_0, \eta_1)$, $D_k(\eta_0, \eta_1)$ are differentiable with respect to η_1 in $(\eta_0, \eta_0 + \zeta)$ with positive derivatives.*

Proof. Setting $y = \frac{\eta - \eta_0}{\eta_1 - \eta_0}$, we write (5.15) in the form

$$\frac{1}{k} = T(C_k, \eta_0, \eta_1) =$$

$$\frac{1}{k}(\eta_1 - \eta_0) \int_0^1 \left\{ \frac{\mu^2}{2} \left[(\eta_1 - \eta_0)^2 y^2 + 2(\eta_1 - \eta_0) y \right] + \right.$$

$$\left. C_k e^{\eta_0} (1 - e^{(\eta_1 - \eta_0) y}) + (\Gamma + C_k \Delta) e^{-\lambda \eta_0} (1 - e^{-\lambda(\eta_1 - \eta_0) y} \right\}^{-\frac{1}{2}} dy. \quad (5.23)$$

We can read it in the form

$$\frac{1}{k} = T(C_k, \eta_0, \eta_1) = \frac{1}{k} \int_0^1 \frac{1}{\sqrt{y(1-y)}} F(y, \eta_0, \eta_1, C_k(\eta_0, \eta_1))\, dy$$

with F bounded and with bounded derivatives with respect to η_1 and C_k. This proves the existence of $\frac{\partial C_k}{\partial \eta_1}$.

Now take $\eta_1' > \eta_1$ and compare $C_k(\eta_0, \eta_1)$ and $C_k(\eta_0, \eta_1')$, which are constructed in such a way to produce the semiperiod $\frac{1}{k}$ in the respective intervals (η_0, η_1), (η_0, η_1'). This implies that the difference $V_{C_k}(\eta_0) - V_{C_k}(\eta)$ cannot be greater or equal to the corresponding difference for the potential associated to the coefficient $C_k(\eta_0, \eta_1')$. Remembering (5.19) we conclude that this would be the case if $C_k(\eta_0, \eta_1) \geq C_k(\eta_0, \eta_1')$. Therefore only the option $C_k(\eta_0, \eta_1) < C_k(\eta_0, \eta_1')$ is left. Now we differentiate the equality $V_{C_k}(\eta_0) = V_{C_k}(\eta)$ with respect to η_1, obtaining

$$\frac{\partial C_k}{\partial \eta_1} e^{\eta_0} + \frac{1}{\lambda} \frac{\partial D_k}{\partial \eta_1} = \frac{\partial V_{C_k}(\eta)}{\partial \eta}_{|\eta = \eta_1} + \frac{\partial C_k}{\partial \eta_1} e^{\eta_1}. \quad (5.24)$$

We have seen that $\frac{\partial C_k}{\partial \eta_1} \geq 0$ and we know that $\frac{\partial V_{C_k}}{\partial \eta}_{|\eta = \eta_1} > 0$. Hence $\frac{\partial D_k}{\partial \eta_1} > 0$. Since we can exchange the role of C_k and D_k, we actually have also $\frac{\partial C_k}{\partial \eta_1} > 0$. □

In view of Theorem 5.2, The following result is obviously interesting

Theorem 5.3. *The limit for $\eta_1 \to \eta_0+$ of the function $\bar{T}(\eta_0, \eta_1)$, defined by (5.21), is bounded if and only if $\eta_0 < \frac{1}{\lambda}$, or $\eta_0 > 1$.*

Proof. Recalling (5.13), two cases must be distinguished:

(I) $H(\eta_0, \eta_1) \geq [-\Gamma]^+$, i.e. $C_0(\eta_0, \eta_1) = \frac{H}{\Delta}$,

(II) $H(\eta_0, \eta_1) < [-\Gamma]^+$, i.e. $C_0(\eta_0, \eta_1) = \frac{[-\Gamma]^+}{\Delta}$.

In case (**I**) the constraint (5.6) is active, meaning that $V_{C_0(\eta_0,\eta_1)}$ takes a maximum in (η_0, η_1) whose values equals $V_{C_0(\eta_0,\eta_1)}(\eta_0)$. Thus for $C \to C_0(\eta_0, \eta_1)+$ the limit of $T(C, \eta_0, \eta_1)$, i.e. $\bar{T}(\eta_0, \eta_1)$, is $+\infty$.

In the second case (5.6) is guaranteed for all $C \geq C_0$, while $C \to C_0+$ makes D tend to zero. Therefore $\bar{T}(\eta_0, \eta_1)$ will be finite.

We keep this in mind while analyzing the limit $\eta_1 \to \eta_0+$.

Let us define:

$$\mathcal{H}(\eta_0) = \lim_{\eta_1 \to \eta_0+} \frac{H(\eta_0, \eta_1)}{\Delta(\eta_0, \eta_1)}. \tag{5.25}$$

We can easily see that

$$\mathcal{H}(\eta_0) = \mu^2 \frac{1}{1+\lambda}(1+\lambda\eta_0)e^{-\eta_0} \tag{5.26}$$

(the limits of $-\Gamma$, Δ are $\frac{\mu^2}{\lambda}\mu_0 e^{\lambda\eta_0}$ and $\frac{1}{\lambda}e^{(1+\lambda)\eta_0}$, respectively, while the limit of the ratio $\left[\frac{\eta^2-\eta_0^2}{\eta_1^2-\eta_0^2} - g(\eta)\right] / \left[\frac{e^\eta - e_0^\eta}{e_1^\eta - e_0^\eta} - g(\eta)\right]$ is $\frac{1}{\eta_0}\frac{1+\lambda\eta_0}{1+\lambda}$).

Similarly we may compute

$$\mathcal{K}(\eta_0) = \lim_{\eta_1 \to \eta_0^+} \frac{[\Gamma]^+}{\Delta} \tag{5.27}$$

which turns out to be

$$\mathcal{K}(\eta_0) = 0 \text{ for } \eta_0 \leq 0, \ \mathcal{K}(\eta_0) = \mu^2 \eta_0 e^{-\eta_0} \text{ for } \eta_0 > 0. \tag{5.28}$$

The limit of $\bar{T}(\eta_0, \eta_1)$ will be finite if and only if $\lim_{\eta_1 \to \eta_0+} C_0(\eta_0, \eta_1) = \mathcal{K}(\eta_0)$, and more precisely if and only if $\mathcal{K}(\eta_0) > \mathcal{H}(\eta_0)$.

On the basis of (5.26), (5.28) the latter inequality is satisfied for $\eta_0 < -\frac{1}{\lambda}$ and for $\eta_0 > 1$. $\square$

Remark 5.1. *According to (5.28) we have that for η_1 sufficiently close to η_0 the following facts hold:*

(i) for $\eta_0 < -\frac{1}{\lambda}$, $C_0(\eta_0, \eta_1)$ is zero, i.e. C can be taken arbitrarily close to zero. Since in addition in the limit $\eta_1 \to \eta_0+$ the relationship (5.7) between C and D becomes

$$D = -\mu^2 \eta_0 e^{\lambda\eta_0} + e^{(1+\lambda)\eta_0} C. \tag{5.29}$$

D has the positive lower bound $D \geq \mu^2 |\eta_0| e^{\lambda\eta_0}$, in the case we are considering.

(ii) For $\eta_0 > 1$, in the limit $\eta_1 \to \eta_0+$, the requirement $D > 0$ acts as a constraint on C, namely $C > \mu^2 \eta_0 e^{-\eta_0}$, which is precisely $C > \mathcal{K}(\eta_0)$. In that case, taking C close to $\mathcal{K}(\eta_0)$ corresponds to having D small.

We can now calculate $T_0(\eta_0) = \lim_{\eta_1 \to \eta_0+} \bar{T}(\eta_0, \eta_1)$ when it is bounded.

First we examine the case

(i) $\eta_0 < \frac{-1}{\lambda}$.

In the limit $\eta_1 \to \eta_0+$, from (5.14) we get

$$\lim_{\eta_1 \to \eta_0+} V_c(\eta) \equiv \bar{V}_c(\eta) = -\frac{1}{2}\mu^2\eta^2 + Ce^\eta + \frac{1}{\lambda}\left[-\mu^2\eta^2 e^{\lambda\eta_0} + Ce^{(1+\lambda)\eta_0}\right] e^{-\lambda\eta}. \tag{5.30}$$

Of course $\bar{V}_c'(\eta_0) = 0$ by construction, and

$$\bar{V}_c''(\eta_0) = -(1 + \lambda\eta_0)\mu^2 + (1 + \lambda)Ce^{\eta_0}. \tag{5.31}$$

For $C = \mathcal{K}(\eta_0) = 0$ we find

$$\bar{V}''_{\mathcal{K}(\eta_0)}(\eta_0) = -(1 + \lambda\eta_0)\mu^2 > 0 \tag{5.32}$$

and the corresponding semiperiod of the linearized oscillations is

$$T_0(\eta_0) = \frac{\pi}{\mu\sqrt{|1 + \lambda\eta_0|}}, \quad \eta_0 < -\frac{1}{\lambda}. \tag{5.33}$$

(ii) Similarly, in case, $\eta_0 > 1$ we use $C = \mathcal{K}(\eta_0) = \mu^2\eta_0 e^{-\eta_0}$ in (5.31), obtaining

$$\bar{V}''_{\mathcal{K}(\eta_0)}(\eta_0) = \mu^2(\eta_0 - 1) \tag{5.34}$$

with the corresponding semiperiod

$$T_0(\eta_0) = \frac{\pi}{\mu\sqrt{\eta_0 - 1}}, \quad \eta_0 > 1. \tag{5.35}$$

For $C > \mathcal{K}(\eta_0)$ in (5.30) the semiperiod $T_{0C}(\eta_0)$ of the linearized oscillations is less than $T_0(\eta_0)$.

In connection with Theorem 5.4 this allows to obtain the following result, which add some information about the existence question.

Theorem 5.4. *If $T_0(\eta_0)$, given either by (5.33) or by (5.35), is greater than $\frac{1}{k}$, then for η_1 sufficiently close to η_0 we can find one unique $C_k(\eta_0, \eta_1)$ to which a class k solution is associated.*

The analysis above facilitates the proof of Theorem 5.1, as pointed out by the following lemma.

Lemma 5.4. *Suppose that for a given η_0 there exists a class k solution for each η_1 in some interval $I = (\eta_0, \eta_0 + \varepsilon)$, to which we associate the total rescaled mass (recall (5.1) and (5.2))*

$$M_k(\eta_0, \eta_1) = M_a + \frac{1}{\lambda}M_b. \tag{5.36}$$

Then

$$\bar{M}_k(\eta_0) \equiv \inf_{\eta_1 \in I} M_k(\eta_0, \eta_1) = \lim_{\eta_1 \to \eta_0+} M_k(\eta_0, \eta_1). \tag{5.37}$$

Proof. A simple expression of $M_k(\eta_0, \eta_1)$ is

$$M_k(\eta_0, \eta_1) = \int_0^1 \left[V_{C_k}\big(\eta(x)\big) + \frac{1}{2}\mu^2\eta^2(x)\right] dx. \tag{5.38}$$

Using

$$\eta'(x) = \sqrt{2}\,[V_{C_k}(\eta_0) - V_{C_k}(\eta)]^{\frac{1}{2}} \tag{5.39}$$

we transform the integral (5.38) to

$$M_k(\eta_0,\eta_1) = \frac{k}{\sqrt{2}} \int_{\eta_0}^{\eta_1} \frac{V_{C_k}(\eta) + \frac{1}{2}\mu^2\eta^2}{\sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}}\, d\eta. \tag{5.40}$$

Adding and subtracting $V_{C_k}(\eta_0)$ to the numerator in the integral and remembering that

$$\frac{1}{\sqrt{2}} \int_{\eta_0}^{\eta_1} \frac{d\eta}{\sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}} = \frac{1}{k}$$

by definition of $C_k(\eta_0,\eta_1)$, we obtain

$$\frac{1}{k} M_k(\eta_0,\eta_1) = \frac{1}{k} V_{C_k}(\eta_0) - \frac{1}{\sqrt{2}} \int_{\eta_0}^{\eta_1} \sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}\, d\eta + \frac{\mu^2}{2\sqrt{2}} \int_{\eta_0}^{\eta_1} \frac{\eta^2}{\sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}}\, d\eta. \tag{5.41}$$

Introducing

$$Z_{C_k}(\eta) = \frac{1}{\sqrt{2}} \int_{\eta_0}^{\eta} \frac{1}{\sqrt{V_{C_k}(\eta_0) - V_{C_k}(\zeta)}}\, d\zeta, \tag{5.42}$$

the last term in (5.41) can be written as

$$\frac{\mu^2}{2} \int_{\eta_0}^{\eta_1} \eta^2 Z'_{C_k}(\eta)\, d\eta \tag{5.43}$$

and it can be integrated by parts, yielding

$$\frac{\mu^2}{2} \eta^2 Z_{C_k}(\eta) \Big|_{\eta_0}^{\eta_1} - \mu^2 \int_{\eta_0}^{\eta_1} \eta Z_{C_k}(\eta)\, d\eta. \tag{5.44}$$

Noting that $Z_{C_k}(\eta_0) = 0$, $Z_{C_k}(\eta_1) = \frac{1}{k}$, we arrive at the following expression

$$\frac{1}{k} M_k(\eta_0,\eta_1) = \frac{1}{k} V_{C_k}(\eta_0) - \frac{1}{\sqrt{2}} \int_{\eta_0}^{\eta_1} \sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}\, d\eta + \frac{1}{2k}\mu^2\eta_1^2 - \mu^2 \int_{\eta_0}^{\eta_1} \eta Z_{C_k}(\eta)\, d\eta. \tag{5.45}$$

Since $Z_{C_k}(\eta) < \frac{1}{k}$ for $\eta \in (\eta_0,\eta_1)$, we see that

$$M_k(\eta_0,\eta_1) > m_k(\eta_0,\eta_1), \quad \eta_1 \in I., \tag{5.46}$$

with

$$m_k(\eta_0,\eta_1) = V_{C_k}(\eta_0) - \frac{1}{\sqrt{2}} \int_{\eta_0}^{\eta_1} \sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}\, d\eta + \frac{1}{2}\mu^2\eta_0^2 \tag{5.47}$$

Moreover

$$\lim_{\eta_1\to\eta_0+} M_k(\eta_0,\eta_1) = \lim_{\eta_1\to\eta_0+} m_k(\eta_0,\eta_1). \tag{5.48}$$

Let us differentiate (5.47) with respect to η_1:

$$\frac{\partial m_k}{\partial \eta_1} = \frac{1}{2}\left(\frac{\partial C_k}{\partial \eta_1}e^{\eta_0} + \frac{1}{\lambda}\frac{\partial D_k}{\partial \eta_1}e^{-\lambda\eta_0}\right) + \frac{k}{2\sqrt{2}}\int_{\eta_0}^{\eta_1} \frac{\frac{\partial C_k}{\partial \eta_1}e^{\eta} + \frac{1}{\lambda}\frac{\partial D_k}{\partial \eta_1}e^{-\lambda\eta}}{\sqrt{V_{C_k}(\eta_0) - V_{C_k}(\eta)}}\,d\eta, \tag{5.49}$$

where we have used once more that the semiperiod is $\frac{1}{k}$.

Thanks to Lemma 5.5 we may conclude that $\frac{\partial m_k}{\partial \eta_1} > 0$. At this point (5.37) follows from (5.46) and (5.48). □

This result brings us very close to the proof of Theorem 5.1, since the bifurcation values for the total biomasses will just be the inf of $\bar{M}_k(\eta_0)$.

Proof of Theorem 5.1. In order to compute $\bar{M}_k(\eta_0)$ we must perform the limit $\eta_1 \to \eta_0+$ in (5.41).

First of all we need to know the limit of $C_k(\eta_0,\eta_1)$.

We can derive it indirectly by imposing that the limit potential, that we denote by $V_k(\eta)$, has a minimum in η_0 and that the linearized oscillations around it have semi-period $\frac{1}{k}$. We satisfy $V_k'(\eta_0) = 0$ automatically taking V_k in the form (5.30), where $C = \bar{C}_k(\eta_0) = \lim_{\eta_1\to\eta_0+} C_k(\eta_0,\eta_1)$. The second condition takes the form

$$V_k''(\eta_0) = (k\pi)^2, \tag{5.50}$$

which defines

$$\bar{C}_k(\eta_0) = \frac{e^{-\eta_0}}{1+\lambda}\left[(k\pi)^2 + (1+\lambda\eta_0)\mu^2\right]. \tag{5.51}$$

At this point we perform the limit in (5.41), obtaining $\frac{1}{k}\bar{M}_k(\eta_0) = \frac{1}{k}V_k(\eta_0) + \frac{\mu^2}{2k}\eta_0^2 = \frac{1}{k}\left[\bar{C}_k(\eta_0)e^{\eta_0}(1+\frac{1}{\lambda}) - \frac{\mu^2}{\lambda}\eta_0\right]$, which leads to the desired expression

$$\bar{M}_k(\eta_0) = \frac{1}{\lambda}\left[(k\pi)^2 + \mu^2 + \mu^2(\lambda-1)\eta_0\right]. \tag{5.52}$$

A first consequence is that for $\lambda = 1$ the total mass $\bar{M}_k$ is independent of η_0, so that

$$\inf \bar{M}_k(\eta_0) = (k\pi)^2 + \mu^2, \text{ for } \lambda = 1. \tag{5.53}$$

When $\lambda \neq 1$ we must look for the extreme admissible values of η_0, by imposing that $\bar{C}_k(\eta_0) > 0$ and that $\bar{D}_k(\eta_0) > 0$, with (see (5.29))

$$\bar{D}_k(\eta_0) = \frac{1}{1+\lambda}\left[(k\pi)^2 + \mu^2 - \mu^2\eta_0\right]e^{\lambda\eta_0}. \tag{5.54}$$

We conclude that η_0 is allowed to vary in the interval

$$\left(-\frac{1}{\lambda} - \frac{1}{\lambda}(\frac{k\pi}{\mu})^2, 1 + (\frac{k\pi}{\mu})^2\right).$$

Hence, for $\lambda > 1$

$$\inf \bar{M}_k(\eta_0) = \frac{(k\pi)^2 + \mu^2}{\lambda^2} \tag{5.55}$$

and for $\lambda < 1$

$$\inf \bar{M}_k(\eta_0) = (k\pi)^2 + \mu^2. \tag{5.56}$$

Thus the theorem is proved, extending the results of [27] for the one population model. $\square$

Remark 5.2. *In the course of the proof above we have seen that the admissible values of* η_0 *corresponding to the existence of a solution which is the limit of class* k *solutions in* (η_0, η_1) *when* $\eta_1 \to \eta_0+$*, belong to the interval* $\left(-\frac{1}{\lambda} - \frac{1}{\lambda}(\frac{k\pi}{\mu})^2, 1 + (\frac{k\pi}{\mu})^2\right)$*. One could ask how this result is related to Theorem 5.6, saying that* $\lim_{\eta_1 \to \eta_0+} \bar{T}(\eta_0, \eta_1)$ *is bounded for* $\eta_0 < -\frac{1}{\lambda}$ *or* $\eta_0 > 1$*.*

In order to understand this detail, let us draw the following curves in the half plane $-\infty < \eta_0 < +\infty$*,* $C > 0$ *(see Figure 5.1):*

(1) $C = \bar{C}_k(\eta_0)$*, i.e. the graph of (5.51);*

(2) $C = -\mu^2 \eta_0 e^{\lambda \eta_0} + e^{(1+\lambda\eta_0)}$*, i.e.* $D = 0$*;*

(3) $V_C''(\eta_0) = 0$*, i.e.* $C = \mu^2 \frac{1+\lambda\eta_0}{1+\lambda} e^{-\eta_0}$*.*

The arc (3) is the singularity set of T*. The points* (η_0, C) *we have used in the proof lie on the arc (1), which has a positive distance from (3) for all* $k \in \mathbb{N}$*.*

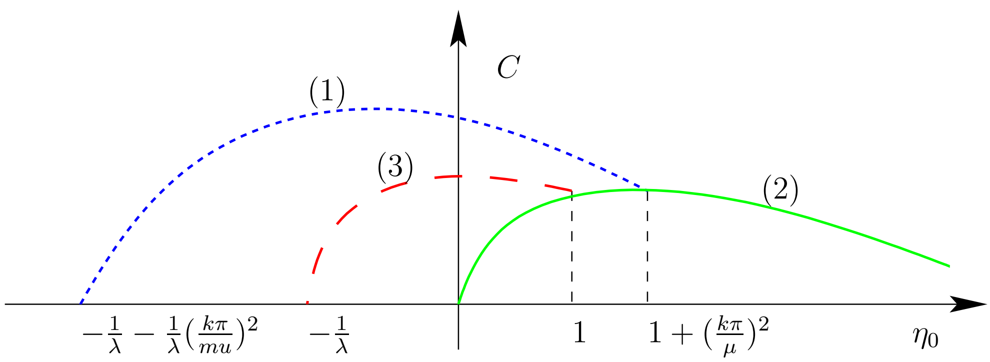


Figure 5.1: Sketch of Remark 5.2.

6. Additional results.

In Theorem 5.1 the situation corresponding to the presence of only one minimum of V (region $\mathcal{B}$) is not fully described because T is generally not monotone in E. Still on the basis of Propositions 3.4 and 3.5 we can assert the following.

For each $(C, D) \in \mathbb{R}^2_+$, let $(V_{min}, +\infty)$ be the range of $V(C, D, \eta)$ and define $T_s(C, D) = \sup_{E \in (V_{min}, +\infty)} T(C, D, E)$. The existence of class k solution is guaranteed for the pair (C, D) starting from $k_{min}(C, D) = min\{k \in \mathbb{N} : T_s(C, D) > \frac{1}{k}\}$. Hence we can state the following theorem

Proposition 6.1. *For $0 < \Theta < +\infty$ consider the family of curves*

$$\Gamma_\Theta = \{(C, D) \in \mathbb{R}^2_+ | T_s(C, D) = \Theta\}.$$

For each $k \in \mathbb{N}$ the existence of class k solutions is guaranteed in the set $\Omega_k = \cup_{\Theta > \frac{1}{k}} \Gamma_\Theta$.

Note that T_s is unbounded for $(C, D) \in \bar{\mathcal{A}}$, so that $\bar{\mathcal{A}} \subset \Omega_k$ for all $k \in \mathbb{N}$. Also, $\Omega_{k'} \subset \Omega_{k''}$ for $k'' > k'$.

Clearly, for Θ large there will be curves Γ_Θ lying in $\mathcal{B}$ below curve (4.8). For such curves the maximum of T is taken for $E \simeq E_i = V(\eta_i)$, η_i being the point of a (nearly horizontal) inflection. Since most of the contribution to $T(C, D, E_i)$ comes from a small neighborhood of η_i, we can look for an approximation of $T(C, D, E_i)$ from below by computing the integral

$$I = \frac{1}{\sqrt{2}} \int_{\eta_i}^{\eta_i + \varepsilon} \frac{d\eta}{\left[-V'(\eta_i)(\eta - \eta_i) - \frac{1}{6} V'''(\eta_i)(\eta - \eta_i)^3\right]^{\frac{1}{2}}}$$

for ε suitably small, where we selected the case in which η_i is less than the coordinate of the minimum of V, i.e. $V'(\eta_i) < 0$, $V''(\eta_i) = 0$, $V'''(\eta_i) < 0$.

We are interested in the case $c = -V'(\eta_i) << 1$. We put $b = -\frac{1}{6} V'''(\eta_i)$ and we write

$$I = \frac{1}{\sqrt{2b}} \int_0^\varepsilon \frac{d\xi}{\sqrt{\alpha\xi + \xi^3}}, \qquad \text{with } \alpha = \frac{6V'(\eta_i)}{V'''(\eta_i)} > 0.$$

If ε is such that $\varepsilon << \alpha$, we can write

$$I \simeq \sqrt{\frac{2\varepsilon}{c}}$$

.

Choosing $\varepsilon = \chi\sqrt{\alpha}$ for some $\chi << 1$, we see that

$$I = (2\chi)^{\frac{1}{2}} (bc)^{-\frac{1}{4}}.$$

As a consequence of the latter formula it is of some interest to draw the lines

$$V' \cdot V''' = \gamma,$$

$$V'' = 0.$$

After some lengthly calculations we find the equations of the branch over which $|V'| << 1$:

$$C = \frac{\mu^2}{1 + \lambda}(1 + \lambda\eta)e^{-\eta} + \frac{\gamma\lambda}{1 + \lambda} \frac{1}{\mu^2(1 - \lambda + \lambda\eta)} e^{-\eta}$$

$$D = \frac{\mu^2}{1+\lambda}(1-\eta)e^{\lambda\eta} + \frac{\gamma}{1+\lambda}\frac{1}{\mu^2(1-\lambda+\lambda\eta)}e^{\lambda\eta}$$

with $\lambda > \frac{4\gamma}{\mu^2}$. Now $C > 0$ requires

$$\eta \in \left(-\frac{1}{\lambda} + \frac{\gamma}{\lambda\mu^4}, 1 - \frac{1}{\lambda} - \frac{\gamma}{\lambda\mu^4}\right) \cup \left(1 - \frac{1}{\lambda}, \infty\right),$$

while $D > 0$ if $\eta < 1 - \frac{\gamma}{\mu^4}$ with $\frac{1}{\lambda} > \frac{4\gamma}{\mu^2}$. Thus we have the restriction $\lambda \in (\frac{4\gamma}{\mu^2}, \frac{\mu^2}{4\gamma})$ and η must vary in the set

$$\left(-\frac{1}{\lambda} + \frac{\gamma}{\lambda\mu^4}, 1 - \frac{1}{\lambda} - \frac{\gamma}{\lambda\mu^4}\right) \cup \left(1 - \frac{1}{\lambda}, 1 - \frac{\gamma}{\mu^4}\right).$$

The two intervals correspond to the cases $V' < 0$, $V''' < 0$ and $V' > 0$, $V''' > 0$.

These lines can be continued above curve (4.8) considering that in the region $\mathcal{B}$ near the vertex of the region $\mathcal{A}$, for each (C, D) the maximum of T practically corresponds to the semiperiod of the linearized oscillations near the minimum of V. Thus we may approximate the curves Γ_Θ with

$$V' = 0,$$

$$V'' = c\mu^2, \quad \text{with } 0 < c << 1$$

i.e. with arcs of (4.48) with $\theta > 1$ and close to 1.

By decreasing Θ the region Ω_Θ expands. We can see that for any $\Theta > 0$ Ω_Θ is bounded.

Let us explore the behavior of the semiperiod at points far from the origin, setting e.g. $D = \delta C$, with $\delta > 0$. Then for C large enough (more precisely $C >> max(\frac{\mu^2}{2}, \frac{\mu^2}{2}\frac{\lambda}{\delta}))$, $V \simeq C(e^\eta + \frac{\delta}{\lambda}e^{-\lambda\eta})$, $V' \simeq -\mu^2\eta + C(e^\eta - \delta e^{-\lambda\eta})$. So V has only one minimum occurring at η_{min} such that $e^{\eta_{min}} \simeq \delta^{\frac{1}{1+\lambda}}$. Thus $V_{min} \simeq C\delta^{\frac{1}{1+\lambda}}\left(1 + \frac{1}{\lambda}\right) := Cf(\delta)$. Taking $E = \Lambda V_{min} = \Lambda C f(\delta)$, $\Lambda > 1$, the semiperiod is given by

$$T \simeq \frac{1}{\sqrt{2}}\frac{1}{\sqrt{C}}\int_{\eta_0}^{\eta_1} \frac{d\eta}{\sqrt{\Lambda f(\delta) - (e^\eta + \frac{\delta}{\lambda}e^{-\lambda\eta})}},$$

and since η_0, η_1, the roots of $V(\eta) = E$, do not depend on C, T tends to zero in all radial directions.

7. Numerical experiments

In this final section we will show numerical simulations to illustrate the behavior of the solutions of system (2.5)-(2.8).

To this end we computed the solution of the evolution problem whose asymptotic limit for long time is expected to satisfy (2.5)-(2.8). The result appears to depend on the total mass in a critical way. Figures 7.1-7.3 are obtained with the same choice of parameters but with a decreasing initial mass of the populations: in the Figure 7.1 the non stationary system tends to a $3-class$ solution; in Figure 7.2,with a smaller initial mass, the asymptotic limit is a $2-class$ solution whereas for an even smaller initial data the initial deviation from constant equilibrium solutions vanishes asymptotically (shown in Figure 7.3). In Figure 7.4 the corresponding plots of p and q are shown.

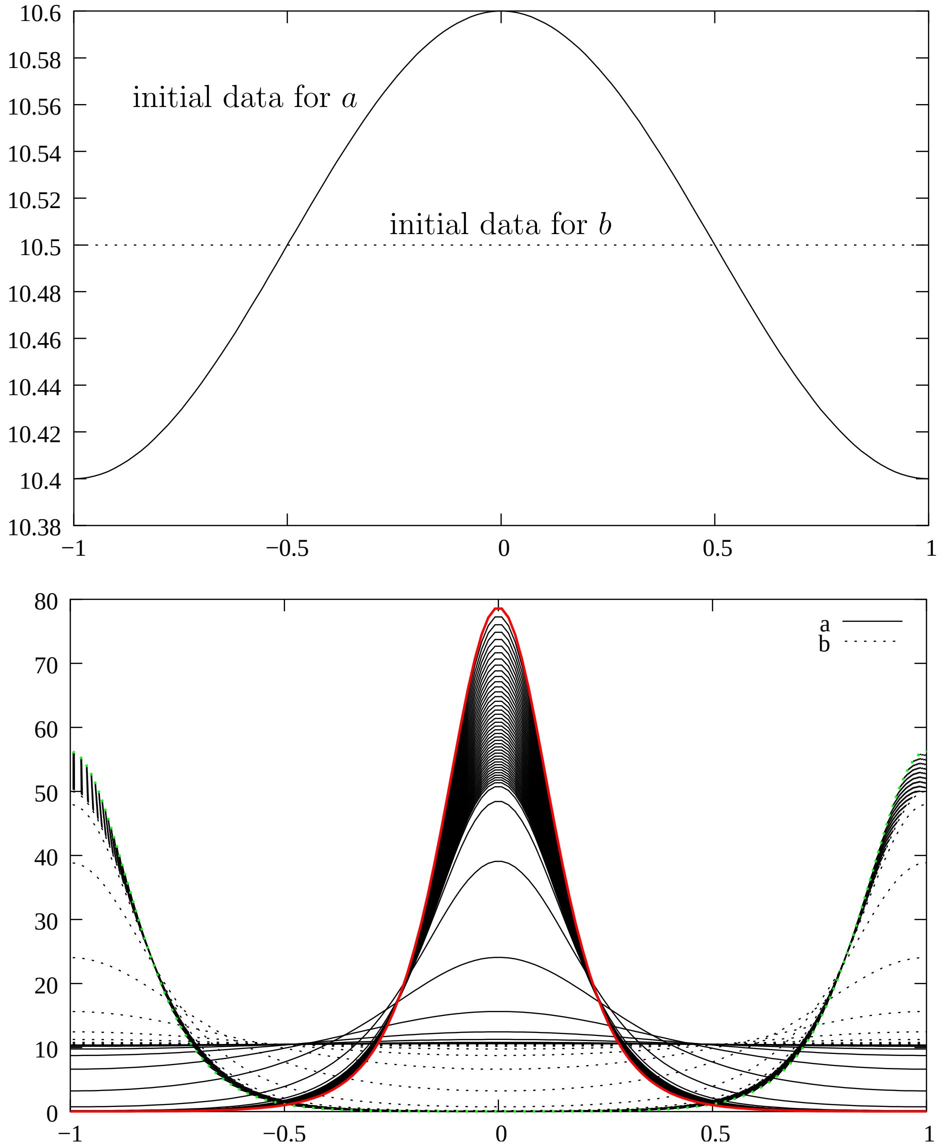


Figure 7.1: $M_a = M_b = 21$.

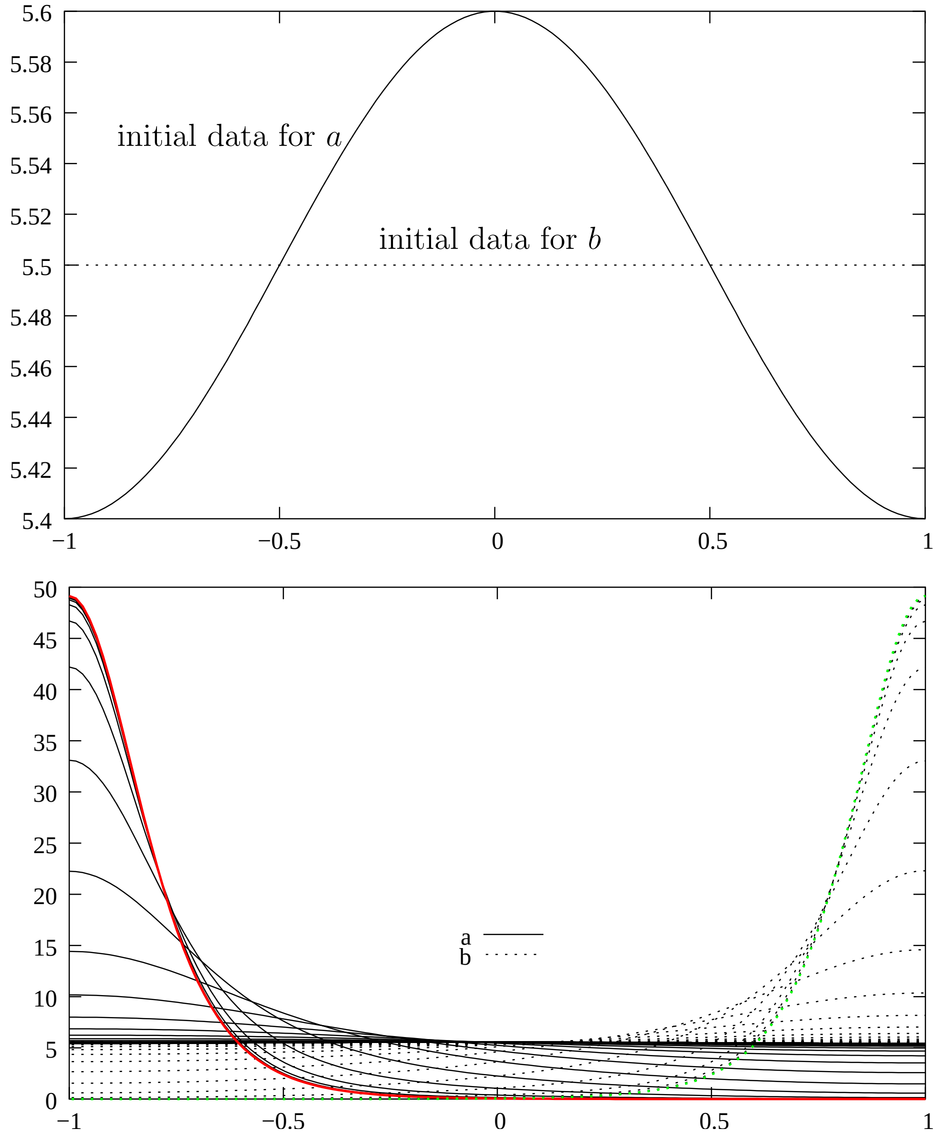
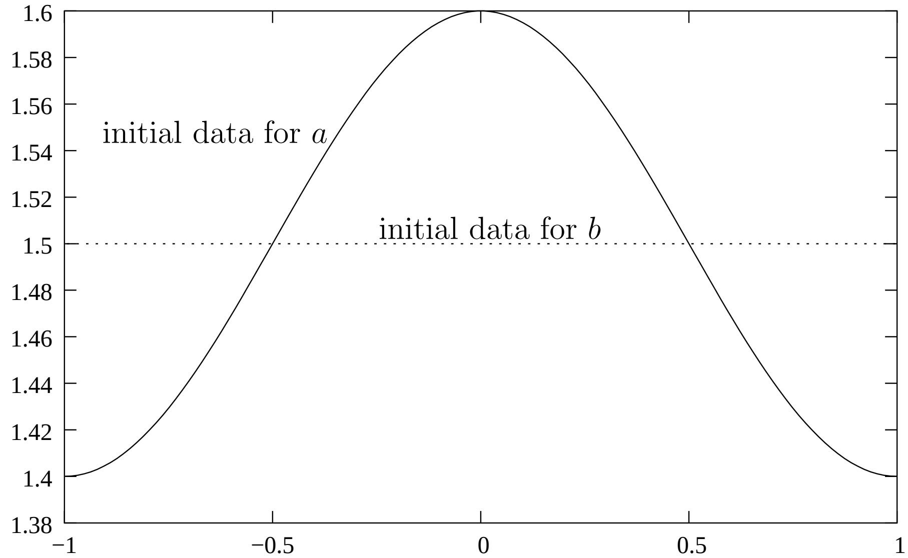


Figure 7.2: $M_a = M_b = 11$.



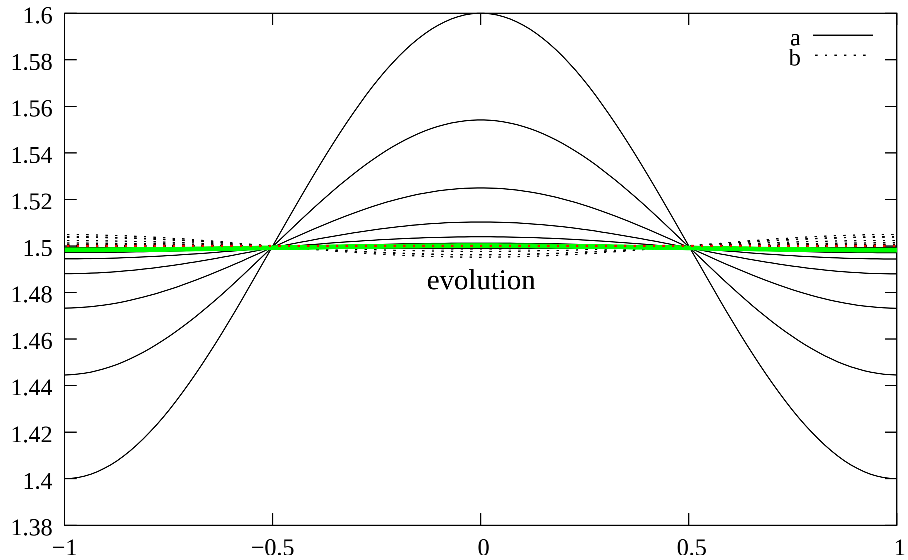


Figure 7.3: $M_a = M_b = 3$.

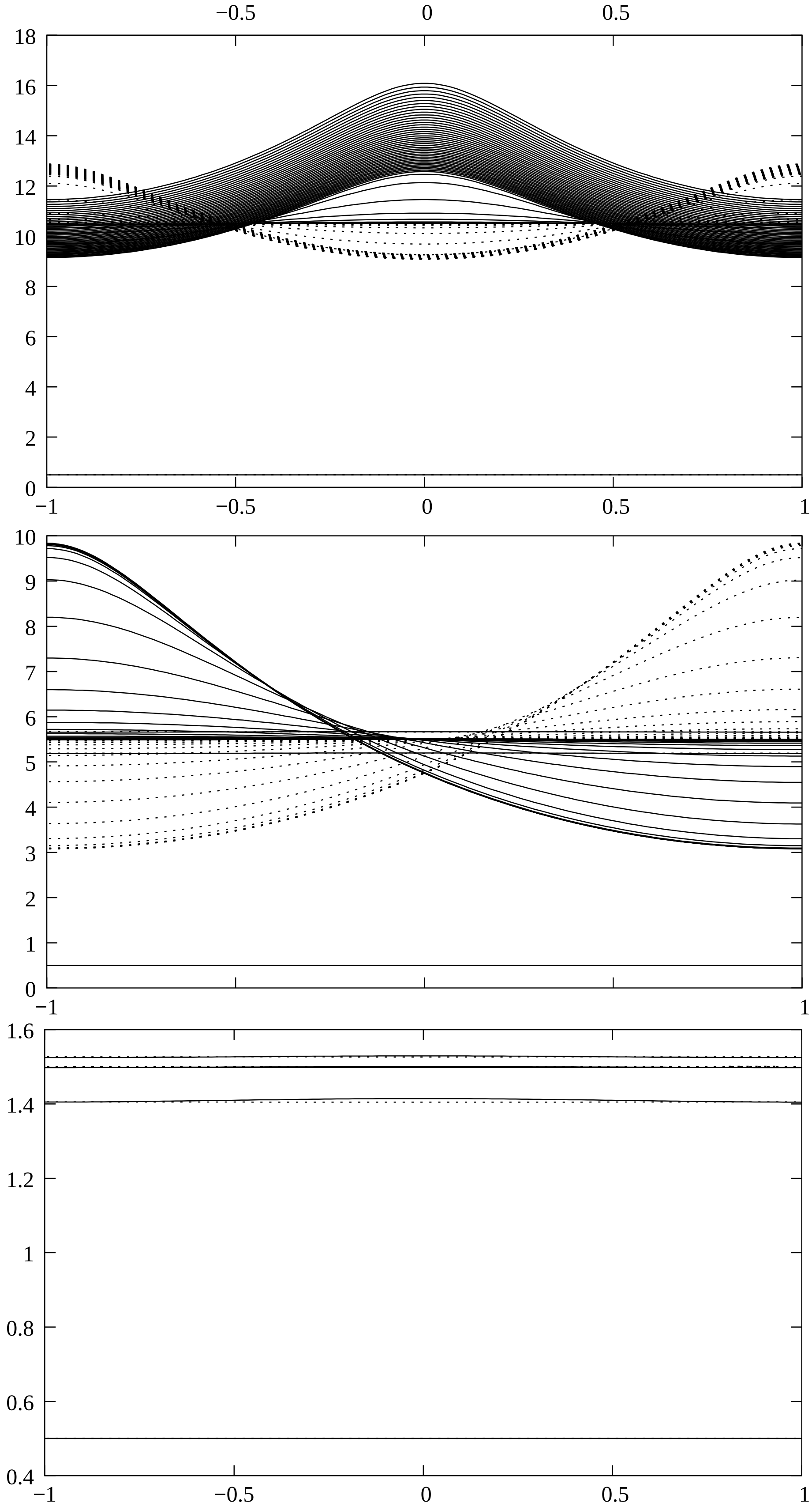


Figure 7.4: Evolution of p and q.

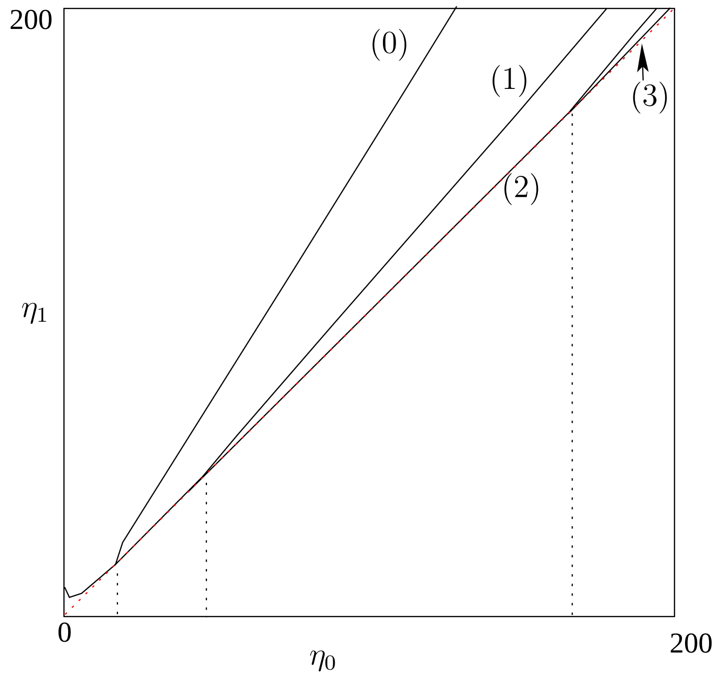


Figure 7.5: Regions in the (η_0, η_1) plane where k-class solutions exist.

Figure 7.5 shows regions in the η_0, η_1 plane where class k solutions exist. According to Theorem 5.1 above the curve (i) only k-class solutions with $k \leq i$ can be found; all the bifurcation points lie on $\eta_0 = \eta_1$ (corresponding to constant solutions).

Finally Figures 7.6 (a),(b) show M_a and M_b versus (η_0, η_1); Figure 7.6 (c) emphasizes a rather peculiar behaviour of $M_a + \frac{1}{\lambda} M_b$ that seems to depend only on $\eta_1 - \eta_0$.

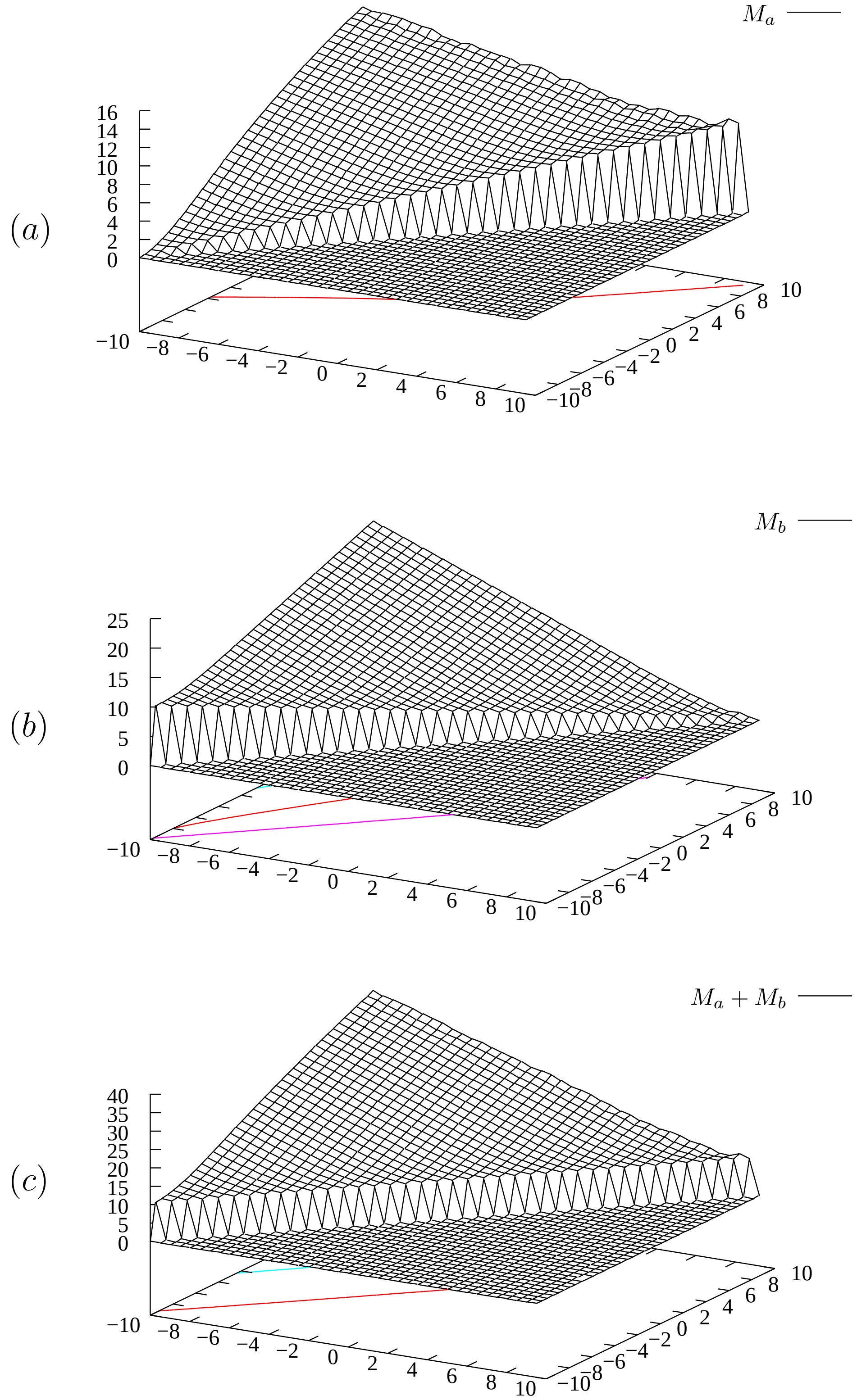


Figure 7.6: Plots of M_a and M_b v.s. extremal values η_0, η_1.

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