3.3 Asymptotic behaviour

The present section is devoted to the study of the asymptotic behaviour of the solution of (3.2). Since the solution of this problem is given, according to the previous section, by

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

in order to simplify the task, we only have to study the dynamics of the autonomous ordinary differential system which is the limit of System (3.5) as t goes to $+\infty$. Afterwards, we easily deduce the behaviour of our initial value problem.

3.3.1 The limit of the nonautonomous ordinary differential system

The goal of this paragraph is to find the limit, at infinity, of the nonautonomous ordinary differential system (3.5). We will be able to apply Markus's theorems (see [59] and [81]), which allows us to determine the dynamics of this nonautonomous ordinary differential system through the study of the asymptotic behaviour of the limiting autonomous ordinary differential system. We need the following results:

Theorem 3.4. *The C^0 linear semigroup $\{S(t), t \geq 0\}$ generated by the operator A is eventually compact. More precisely, $S(t)$ is compact for any $t \geq l$.*

Proof. For all $t \geq l$, we have $S(t) = S(t-l)S(l)$. The operators $\{S(t), t \geq 0\}$ are all bounded, so we only have to prove that $S(l)$ is compact in order to show this result. We have, using 2.3,

$$\begin{aligned} S(l)(u_0, v_0)(a) &= \begin{pmatrix} S_1(l)(u_0, v_0)(a) \\ S_2(l)(u_0, v_0) \end{pmatrix} \\ &= \begin{pmatrix} bv_0 e^{-\nu(l-a)} + b\int_0^{l-a} e^{-\nu(l-a-s)} u_0(l-s)ds \\ \\ v_0 e^{-\nu l} + \int_0^l e^{-\nu(l-s)} u_0(l-s)ds \end{pmatrix}. \end{aligned}$$

Let now F be a bounded subset of $L^1[0, l] \times \mathbb{R}$, and let us show that $S_1(l)F$ and $S_2(l)F$ are precompact. The second set is obviously bounded in $\mathbb{R}$, so $S_2(l)F$ is precompact.

We have, assuming that $\omega = (\eta, l-\eta), 0 < \eta < l$, the following, for h sufficiently small,

$$\int_\eta^{l-\eta} |S_1(l)(u_0,v_0)(a+h) - S_1(l)(u_0,v_0)(a)|\, da =$$

$$= \int_\eta^{l-\eta} \left| bv_0 e^{-\nu(l-a-h)} + b\int_0^{l-a-h} e^{-\nu(l-a-h-s)} u_0(l-s)ds - \right.$$

$$\left. -bv_0 e^{-\nu(l-a)} - b\int_0^{l-a} e^{-\nu(l-a-s)} u_0(l-s)ds \right| da \longrightarrow 0$$

uniformly for $(u_0, v_0) \in F$ as h tends to 0. We also have

$$\begin{aligned}
\int_{[0,l]\backslash\omega} |S_1(l)(u_0,v_0)(a)|\, da &= \int_0^\eta |S_1(l)(u_0,v_0)(a)|\, da + \int_{l-\eta}^l |S_1(l)(u_0,v_0)(a)|\, da \\
&= \int_0^\eta \left| bv_0 e^{-\nu(l-a)} + b\int_0^{l-a} e^{-\nu(l-a-s)} u_0(l-s)ds \right| da \\
&\quad + \int_{l-\eta}^l \left| bv_0 e^{-\nu(l-a)} + b\int_0^{l-a} e^{-\nu(l-a-s)} u_0(l-s)ds \right| da \\
&\leq \eta bv_0 + b\int_0^\eta \int_0^{l-a} |u_0(l-s)|\, dsda \\
&\quad + \eta bv_0 + b\int_{l-\eta}^l \int_0^{l-a} |u_0(l-s)|\, dsda \longrightarrow 0
\end{aligned}$$

as η tends to 0 uniformly for $(u_0, v_0) \in F$. Hence by a standard compactness criterion in L^p-spaces (see Corollary IV.26, p. 74 in [14]), $S(l)F$ is precompact, i.e. $S(l)$ is compact. $\square$

Remark 3.2. *From this theorem, it immediately follows that the $\alpha-$growth bound of $\{S(t), t \geq 0\}$, $\omega_1(A) := \lim_{t\to\infty} \frac{1}{t}\log(\alpha[S(t)])$, equals $-\infty$, where α is the measure of noncompactness (see [86]).*

Theorem 3.5. *Let $\Phi \in L^1[0,l] \times \mathbb{R}$, then it follows that*

$$\lim_{t\to\infty} e^{-\lambda^* t} S(t)\Phi = P\Phi \tag{3.6}$$

where

$$P\Phi = \frac{1}{2\pi i}\int_\Gamma (\lambda - A)^{-1}\, \Phi d\lambda = \frac{\Phi_2 + \int_0^l e^{-\lambda^*(l-s)}\Phi_1(s)ds}{1 + ble^{-\lambda^* l}}\varphi =: c(\Phi_1, \Phi_2)\varphi$$

where $\varphi(a) = \left(be^{-\lambda^* a}, 1\right)$ is an eigenvector of the operator A associated to λ^*, and Γ is a positively oriented closed curve in C enclosing λ^*, but no other point of $\sigma(A)$. (notice that $P\varphi = \varphi$ and, hence, P is a projection operator)

Proof. Let $\Lambda := \{\lambda^*\}$ and $\omega \in$ R such that

$$\sup_{\substack{\lambda \in VP(A) \\ \lambda \neq \lambda^*}} Re\lambda < \omega < \lambda^*.$$

Let $P_0 := I - P$, $M_0 := R(P_0)$, $M := R(P)$ where $R(P_0)$ and $R(P)$ are respectively the projection of X by P_0 and P, and let $E\sigma(A)$ be the essential spectrum of A. Then

$$\begin{array}{rcl} \omega_{2,1} & := & \max\left(\omega_1(A), \sup_{\lambda\in\sigma(A)\setminus E\sigma(A)\setminus\Lambda} Re\lambda\right) \\ & \leq & \max\left(\omega_1(A), \sup_{\lambda\in\sigma(A)\setminus\Lambda} Re\lambda\right) < \omega. \end{array}$$

Moreover λ^* is a simple pole of the operator $(\lambda I - A)^{-1}$. So, we get from the projection theorem (see [87] or [86], p. 180) that
(1) $X = M \oplus M_0$,
(2) there exists a constant $K \geq 1$ such that,

$$|S(t)P_0\Phi|_X \leq Ke^{\omega t}\,|P_0\Phi|_X \qquad \forall \Phi \in X \quad \text{and} \quad \forall t \geq 0$$

(3) the restriction of the operator A to M denoted by A_M is bounded and $S(t)/_M = e^{tA_M}$
(4) $M = N(\lambda^* I - A)$, i.e. $\Phi \in M$ if and only if $A\Phi = \lambda^*\Phi$.
From this it follows that

$$S(t)\Phi = e^{tA_M}\Phi = e^{\lambda^* t}\Phi, \qquad \forall \Phi \in M \quad \text{and} \quad \forall t \geq 0.$$

Therefore, for any $\Phi \in X$,

$$\begin{array}{rcl} \left|e^{-\lambda^* t}S(t)\Phi - P\Phi\right|_X & = & \left|e^{-\lambda^* t}S(t)P\Phi + e^{-\lambda^* t}S(t)P_0\Phi - P\Phi\right|_X \\ & = & \left|e^{-\lambda^* t}S(t)P_0\Phi\right|_X \leq Ke^{(\omega-\lambda^*)t}|P_0\Phi|_X, \end{array}$$

hence (3.6). Now let us compute $P\Phi$ using some results of complex analysis. So initially we have that

$$(\lambda I - A)^{-1}\Phi = \begin{pmatrix} u \\ v \end{pmatrix}$$

is equivalent to

$$(\lambda I - A)\begin{pmatrix} u \\ v \end{pmatrix} = \Phi.$$

That is,

$$\begin{cases} \frac{du}{da} + \lambda u &= \Phi_1 \\ \\ \lambda v - u(l) &= \Phi_2 \\ \\ u(0) &= bv. \end{cases}$$

It is clear that the solution of this system is

$$u(a) = bve^{-\lambda a} + \int_0^a e^{-\lambda(a-x)}\Phi_1(x)dx$$

and

$$v = \frac{\Phi_2 + \displaystyle\int_0^l e^{-\lambda(l-x)}\Phi_1(x)dx}{\lambda - be^{-\lambda l}}.$$

Let P_1, P_2, Q and R_1 be complex functions such that

$$\begin{aligned} P_1(\lambda) &:= be^{-\lambda a}(\Phi_2 + \int_0^l e^{-\lambda(l-x)}\Phi_1(x)dx) \\ P_2(\lambda) &:= \Phi_2 + \int_0^l e^{-\lambda(l-x)}\Phi_1(x)dx \\ Q(\lambda) &:= \lambda - be^{-\lambda l} \\ R_1(\lambda) &:= \int_0^a e^{-\lambda(a-x)}\Phi_1(x)dx. \end{aligned}$$

Therefore,

$$u(a) = \frac{P_1(\lambda)}{Q(\lambda)} + R_1(\lambda)$$

and

$$\int_\Gamma u d\lambda = \int_\Gamma \frac{P_1(\lambda)}{Q(\lambda)} d\lambda + \int_\Gamma R_1(\lambda)d\lambda.$$

Since the function R_1 is holomorphic then

$$\int_\Gamma R_1(\lambda)d\lambda = 0$$

and

$$\int_\Gamma u d\lambda = \int_\Gamma \frac{P_1(\lambda)}{Q(\lambda)} d\lambda = 2\pi i Res\left(\frac{P_1}{Q}, \lambda^*\right)$$

because Q vanishes only at λ^*. We also have

$$\int_\Gamma v d\lambda = \int_\Gamma \frac{P_2(\lambda)}{Q(\lambda)} d\lambda = 2\pi i Res\left(\frac{P_2}{Q}, \lambda^*\right).$$

On the other hand $P_1(\lambda^*) \neq 0, P_2(\lambda^*) \neq 0$ and $Q(\lambda^*) = 0$ imply that

$$Res\left(\frac{P_1}{Q}, \lambda^*\right) = \frac{P_1(\lambda^*)}{Q'(\lambda^*)} = \frac{P_1(\lambda^*)}{1 + ble^{-\lambda^* l}}$$

and

$$Res\left(\frac{P_2}{Q}, \lambda^*\right) = \frac{P_2(\lambda^*)}{Q'(\lambda^*)} = \frac{P_2(\lambda^*)}{1 + ble^{-\lambda^* l}}.$$

Then

$$\begin{aligned} P\Phi &= \frac{1}{2\pi i}\left(\int_\Gamma u d\lambda, \int_\Gamma v d\lambda\right) \\ &= \frac{1}{1 + ble^{-\lambda^* l}} \left(P_1(\lambda^*), P_2(\lambda^*)\right) \\ &= \frac{\Phi_2 + \int_0^a e^{-\lambda^*(l-x)}\Phi_1(x)dx}{1 + ble^{-\lambda^* l}} \left(be^{-\lambda^* a}, 1\right) \\ &= c(\Phi_1, \Phi_2)\varphi(a)\Box. \end{aligned}$$

Now, from this, the following result easily follows

Corollary 3.1. *The limit of the asymptotically autonomous ordinary differential system (3.5) when t goes to infinity is the following autonomous ordinary differential system*

$$\left\{ \begin{array}{rcl} r' &=& g(r)r - f(\psi)\tilde{g}(r), \\ \psi' &=& \left(\lambda^* - m(r)\right)\psi, \end{array} \right. \tag{3.7}$$

where the real function f is defined as $f(\psi) := h\left(L\left(\psi c(u_0, v_0)\varphi\right)\right) = h\left(\psi c(u_0, v_0) L\varphi\right)$.

Remark 3.3. *Notice that, according to the hypotheses satisfied by the functions h and L, the function f is strictly increasing, unbounded and vanishes at 0 if $c(u_0, v_0) > 0$ and this latter fact holds if (u_0, v_0) is a positive nonvanishing initial condition.*

Now let us start the study of the asymptotic behaviour of the autonomous ordinary differential system (3.7).

3.3.2 Equilibrium points of the autonomous ordinary differential system and their stability

In this subsection we first state a result which shows that under a condition on λ^*, the (positive) solutions of the autonomous ordinary differential system (3.7) are bounded. After that we determine the equilibrium points of this system and their stability. When a coexistence equilibrium point exists and the function $\tilde{g}(r)$ is any increasing smooth function it is difficult to determine exactly the dynamics of the previous system. However, assuming that $\tilde{g}(r) = r$, we will prove that this coexistence steady state is a global attractor.

We state the following proposition without proof because it is a particular case of Proposition 3.4 below (in Sect. 3.3.3).

Proposition 3.2. *If $\lambda^* < m(0)$ then all the (positive) solutions of the autonomous ordinary differential equations system (3.7) are bounded.*

Let us now undertake the study of the asymptotic behaviour of the autonomous ordinary system differential (3.7). Its steady states are the solutions of the following system

$$\left\{ \begin{array}{lcl} g(r)r - f(\psi)\tilde{g}(r) & = & 0 \\ (\lambda^* - m(r))\,\psi & = & 0. \end{array} \right.$$

It is clear that $(0,0)$, $(r_c, 0)$ and, in the case that $\lambda^* = m(0)$, $(0,\psi)$, $\forall \psi > 0$, are steady states. The remaining ones satisfy

$$\left\{ \begin{array}{l} g(r)r = f(\psi)\tilde{g}(r) \\ m(r) = \lambda^*. \end{array} \right.$$

This system has a unique solution (r_e, ψ_e) not included among the preceding ones and such that $\psi_e = f^{-1}\left(g(r_e)r_e/\tilde{g}(r_e)\right)$, if and only if $m(r_e) = \lambda^*$ and $0 < r_e < r_c$.

Let now the matrix $L(r,\psi)$ be defined by

$$L(r,\psi) = \begin{pmatrix} g'(r)r + g(r) - f(\psi)\tilde{g}'(r) & -f'(\psi)\tilde{g}(r) \\ & \\ -m'(r)\psi & \lambda^* - m(r) \end{pmatrix}.$$

So let $\lambda \in \mathbb{C}$ be such that

$$\det(L(0,0)-\lambda I) = \begin{vmatrix} g(0)-\lambda & 0 \\ 0 & \lambda^*-m(0)-\lambda \end{vmatrix} = (g(0)-\lambda)(\lambda^*-m(0)-\lambda)=0$$

and

$$\det(L(r_c,0)-\lambda I) = \begin{vmatrix} g'(r_c)r_c-\lambda & -f'(0)\tilde{g}(r_c) \\ 0 & \lambda^*-m(r_c)-\lambda \end{vmatrix} = (g'(r_c)r_c-\lambda)(\lambda^*-m(r_c)-\lambda)=0.$$

Using the linearization principle and the Poincaré-Bendixson theorem, it is easy to see that:

- If $\lambda^* \le m(r_c)$ then the asymptotic behaviour is very simple: there are only two steady states: the saddle point $(0,0)$, and $(r_c,0)$ which is a stable node. On the other hand, since all the positive solutions are bounded, this last equilibrium point is the global attractor except for the half axis $r=0, \psi \ge 0$.

- If $\lambda^* > m(0)$, then $(0,0)$ becomes a source and $(r_c,0)$ becomes a saddle point, and all the trajectories are unbounded except those contained in the half axis $\psi = 0, r \ge 0$.

- If $\lambda^* = m(0)$ then, a simple analysis of the vector field shows that all the solutions are bounded. Furthermore, any solution with initial condition not belonging to the half axis $r \ge 0, \psi = 0$, tends to an equilibrium point $(0,\psi)$ where $\psi > 0$ depends on the initial condition.

Finally, we study the more interesting case where $\lambda^* = m(r_e)$ and $0 < r_e < r_c$. There are, in this case, only three steady states $(0,0), (r_c,0)$ and (r_e,ψ_e); $\psi_e =$

$f^{-1}(g(r_e)r_e/\tilde{g}(r_e))$. First of all, we immediately see that $(0,0)$ and $(r_c, 0)$ are saddle points. On the other hand we have that

$$\begin{aligned} \det(L(r_e,\psi_e)-\lambda I) &= \begin{vmatrix} g'(r_e)r+g(r_e)-f(\psi_e)\tilde{g}'(r_e)-\lambda & -f'(\psi_e)\tilde{g}(r_e) \\ \\ -m'(r_e)\psi_e & -\lambda \end{vmatrix} \\ \\ &= \lambda^2-(g'(r_e)r+g(r_e)-f(\psi_e)\tilde{g}'(r_e))\,\lambda \\ \\ &\quad -m'(r_e)\psi_e f'(\psi_e)\tilde{g}(r_e)=0 \end{aligned}$$

implies that

$$\begin{aligned} \lambda &= \frac{g'(r_e)r+g(r_e)-f(\psi_e)\tilde{g}'(r_e)}{2} \\ &\pm\frac{\sqrt{(g'(r_e)r+g(r_e)-f(\psi_e)\tilde{g}'(r_e))^2+4m'(r_e)\psi_e f'(\psi_e)\tilde{g}(r_e)}}{2}. \end{aligned}$$

Let now $G(r)=f^{-1}(g(r)r/\tilde{g}(r))$, so

$$\begin{aligned} G'(r_e) &= (f^{-1})'\left(\frac{g(r_e)r_e}{\tilde{g}(r_e)}\right)\frac{(g'(r_e)r_e+g(r_e))\tilde{g}(r_e)-\tilde{g}'(r_e)g(r_e)r_e}{(\tilde{g}(r_e))^2} \\ &= (f^{-1})'\left(\frac{g(r_e)r_e}{\tilde{g}(r_e)}\right)\frac{g'(r_e)r_e+g(r_e)-f(\psi_e)\tilde{g}'(r_e)}{\tilde{g}(r_e)}. \end{aligned}$$

Since the function f is increasing and $\tilde{g}(r_e)>0$ then the term $K:=\frac{\tilde{g}(r_e)}{(f^{-1})'\left(\frac{g(r_e)r_e}{\tilde{g}(r_e)}\right)}$ is also positive. So, we can write

$$\lambda=\frac{KG'(r_e)\pm\sqrt{(KG'(r_e))^2+4m'(r_e)\psi_e f'(\psi_e)\tilde{g}(r_e)}}{2}.$$

Now it is clear that the stability of the coexistence equilibrium point (r_e,ψ_e) depends on the derivative of the function G at r_e and the proof of the following is straightforward

Theorem 3.6. *If $\lambda^*=m(r_e)$ and $0<r_e<r_c$ holds then the coexistence steady state (r_e,ψ_e) of the autonomous two dimensional system (3.7) is asymptotically stable if $G'(r_e)<0$ and it is unstable if $\bar{G}'(r_e)>0$.*

Now, using this last theorem, the Poincaré-Bendixson Theorem yields immediately the following results which give some ideas about the possible dynamics of the autonomous two dimensional system (3.7).

Corollary 3.2. *Let us assume that $\lambda^* \in (m(r_c), m(0))$, i.e., that (3.7) has a unique coexistence equilibrium point (r_e, ψ_e) such that $0 < r_e < r_c$, $\lambda^* = m(r_e)$ and $\psi_e = f^{-1}(g(r_e))$. Then the two following results hold*

i) If $G'(r_e) > 0$ then there exists at least a limit cycle surrounding the coexistence steady state (r_e, ψ_e) of System (3.7). Furthermore if the closed orbits of this system are all isolated then any solution of (3.7), with initial conditions $(r_0, 1) \neq (r_e, \psi_e)$ such that $r_0 > 0$, tends to one of these periodic orbits.

ii) Let us assume that $G'(r_e) < 0$. If System (3.7) has no periodic orbit then the coexistence equilibrium point (r_e, ψ_e) is a global attractor of the solutions corresponding to the initial conditions $(r_0, 1)$ with $r_0 > 0$. Otherwise, let us assume that the (existing) closed orbits are all isolated. Then (r_e, ψ_e) is the ω-limit of all the solutions of System (3.7) enclosed by the first closed orbit and any other solution such that $r_0 > 0$ tends to one of these periodic orbits.

Finally, let us study the stability of the coexistence steady state (r_e, ψ_e) of System (3.7) in a the special case $\tilde{g}(r) = r$. We now consider the following function $W : \mathbb{R}_+ \times \mathbb{R}_+ \longrightarrow \mathbb{R}$ defined by

$$W(r, \psi) = \lambda^* \log r - \int_1^r \frac{m(x)}{x} dx - f(\psi_e) \log \psi + \int_1^\psi \frac{f(x)}{x} dx.$$

Taking the time derivative of ω, we get

$$\begin{aligned}\dot{W}(r, \psi) &= \left(\tfrac{\lambda^* - m(r)}{r}, \tfrac{f(\psi) - f(\psi_e)}{\psi}\right) \cdot \left((g(r) - f(\psi))\, r, (\lambda^* - m(r))\, \psi\right) \\ &= (\lambda^* - m(r))\,(g(r) - f(\psi_e)) = (\lambda^* - m(r))\,(g(r) - g(r_e)) \leq 0\end{aligned}$$

because the two factors have opposite signs if $r \neq r_e$ (and both vanish if $r = r_e$). On the other hand we have

$$\begin{aligned}\tfrac{\partial W}{\partial r}(r, \psi) &= \tfrac{\lambda^* - m(r)}{r} &> 0 \quad \text{if and only if} \qquad r > r_e, \\ \tfrac{\partial W}{\partial \psi}(r, \psi) &= \tfrac{f(\psi) - f(\psi_e)}{\psi} &> 0 \quad \text{if and only if} \qquad \psi > \psi_e.\end{aligned}$$

Therefore the point (r_e, ψ_e) is the absolute minimum of W. Hence $\tilde{W}(r,\psi) = W(r,\psi) - W(r_e,\psi_e)$ is a global Liapunov function and (r_e,ψ_e) is a stable equilibrium. We note that there are not limit cycles. This follows from [43, Chp. 11] because $\tilde{W}$ is not constant on any open set.

The following is the phase portrait of (3.7)

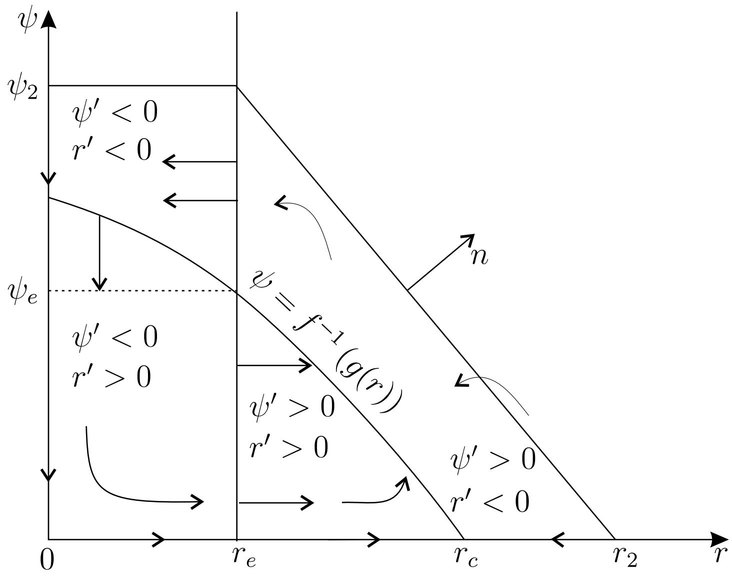

Figure 3.1: The phase portrait of (3.7) in the case $\tilde{g}(r) \equiv r$

Now it follows

Proposition 3.3. *If* $\lambda^* \in (m(r_e), m(0))$*, then the steady state* (r_e, ψ_e) *of System (3.7) with* $\tilde{g}(r) = r$ *is a global attractor for the solutions* (r,ψ) *such that* $r > 0$ *and* $\psi > 0$.

Proof. Let the open subsets U_α, $\alpha > 0$ of $\mathbb{R}_+ \times \mathbb{R}_+$ be given by:

$$U_\alpha = \{(r,\psi) \in \mathbb{R}_+ \times \mathbb{R}_+ \,; \tilde{W}(r,\psi) < \alpha\}$$

such that $\tilde{W}$ is a Liapunov's function in $\overline{U}_\alpha$. Let also

$$E_\alpha := \left\{ x; \dot{\tilde{W}}(x) = 0, x \in \overline{U}_\alpha \right\}.$$

Firstly, it is easy to see that all the straight lines passing through (r_e, ψ_e), cross the level curve $\alpha > 0$ of $\tilde{W}$ exactly in two points. Consequently this level curve is a closed curve surrounding U_α. On the other hand, U_α is positively invariant, moreover $\{(r_e, \psi_e)\}$ is the unique invariant subset of E_α. Then, according to the theorem of LaSalle,(see [52]), (r_e, ψ_e) is a global attractor in U_α. As for all $(x, y) \in \mathbb{R}_+ \times \mathbb{R}_+$ there exists $\alpha > 0$ such that $(x, y) \in U_\alpha$, the statement follows. $\square$

3.3.3 The dynamics of the nonautonomous ordinary differential system

In this section, using the results of the previous subsection, we study the dynamics of the nonautonomous ordinary differential system (3.5) applying the following Markus theorems (see [59], [62], [81]):

Theorem 3.7. *(Markus) The ω-limit set ω of a forward bounded solution x of an asymptotically autonomous ordinary differential equation is non-empty, compact, and connected. Moreover, ω attracts x.*

Theorem 3.8. *(Markus) Let e be a locally asymptotically stable equilibrium of an autonomous ordinary differential equation which is the limit of a nonautonomous ordinary differential equation and ω the ω-limit set of a forward bounded solution x of this last nonautonomous equation. If ω contains a point y_0 such that the solution y of the autonomous ordinary differential equation, with $y(0) = y_0$, converges to e for $t \to +\infty$, then $w = \{e\}$, i.e., $x(t) \to e, t \to +\infty$.*

Theorem 3.9. *(Markus) Let ω be the ω-limit set of a forward bounded solution of a nonautonomous ordinary differential equation. Then ω either contains at least one equilibrium of the limit of this nonautonomous ordinary differential equation or ω is the union of periodic orbits of this limit equation.*

We note that this last Markus theorem generalizes the Poincaré-Bendixson Theorem to asymptotically autonomous planar systems.

First of all, let us prove the important following result

Proposition 3.4. *Let us assume $\lambda^* < m(0)$. Then all the positive solutions of the nonautonomous ordinary system (3.5) are bounded.*

Proof. First, the result is obvious if $\lambda^* < m(r)$ for all r. Else, let $C_{r_2,p}$ be the convex envelope of vertices $(0,0),(r_2,0),(r_e,\psi_2)$ and $(0,\psi_2)$, where $r_2 > r_e$, $m(r_e) = \lambda^*$ and $\psi_2 > f^{-1}(g(0))$. Let n be the unitary vector orthogonal to the segment L of extremes $(r_2,0)$ and (r_e,ψ_2) pointing to the exterior of $C_{r_2,p}$, and let $v(t)$ be the tangent vector to the trajectories at time t. We have $(r,\psi) \in L$ if and only if $((r,\psi) - (r_2,0)) \cdot n = 0$ and $r_e < r < r_2$, i.e., if $n = (n_1,n_2)$ then $\psi = (r_2 - r)n_1/n_2 = (r_2 - r)p$ where $p = n_1/n_2$. Now we will prove that for $r_2 > r_c$, $C_{r_2,p}$ is positively invariant if p is large enough. It is sufficient to show that, whenever $\psi(t) = (r_2 - r(t))\,p$, $r(t) \in (r_e, r_2)$, we have $v(t) \cdot n < 0$, i.e., the trajectories do not go out when they touch L. We get

$$v(t) \cdot n = \left(g(r)r - h\left(L\left(\psi\tilde{S}(t)(u_0,v_0)\right)\right)\right)\tilde{g}(r)n_1 + (\lambda^* - m(r))\,\psi n_2,$$

so $v(t) \cdot n < 0$ if and only if

$$\left(h\left(L\left(\psi\tilde{S}(t)(u_0,v_0)\right)\right)\tilde{g}(r) - g(r)r\right)n_1 > (\lambda^* - m(r))\,\psi n_2.$$

As $\lambda^* - m(r) > 0$ for $r \in (r_e, r_c)$, the last equality is equivalent to

$$\begin{aligned} & (\lambda^* - m(r))^{-1}\left(h\left(L\left(\psi\tilde{S}(t)(u_0,v_0)\right)\right)\tilde{g}(r) - g(r)r\right)n_1/\psi n_2 \; = \\ = \; & (\lambda^* - m(r))^{-1}(r_2 - r)^{-1}\left(h\left(L\left(p(r_2 - r)\tilde{S}(t)(u_0,v_0)\right)\right)\tilde{g}(r) - g(r)r\right) > 1. \end{aligned}$$

Notice that if $(u_0,v_0) \neq (0,0)$ then Theorem (3.5) implies that there exists $k > 0$ such that

$$L\left(\tilde{S}(t)(u_0,v_0)\right) \geq k.$$

Hence, it suffices to prove that, for $r \in (r_e, r_2)$,

$$F(r,p) := \frac{h\left(p(r_2 - r)k\right)\tilde{g}(r) - g(r)r}{(\lambda^* - m(r))\,(r_2 - r)} > 1.$$

It is obvious that there exists $\varepsilon_0(r_2) > 0$ such that for all $r \in (r_2 - \varepsilon_0, r_2)$ we have

$$\frac{h\left(p(r_2 - r)k\right)\tilde{g}(r) - g(r)r}{(\lambda^* - m(r))\,(r_2 - r)} > 1$$

for any $p > 0$.

For $r \in (r_e, r_2 - \varepsilon_0]$ we get

$$h\left(p(r_2 - r)k\right)\tilde{g}(r) - g(r)r \geq h\left(p(r_2 - r)k\right)\tilde{g}(r_e) - g(r_e)r_e$$

because $\tilde{g}$ and g are increasing and decreasing functions respectively. Moreover there exists a constant $M(r_2)$ such that $0 < (\lambda^* - m(r))\,(r_2 - r) \le M(r_2),\ \forall r \in (r_e, r_2 - \varepsilon_0]$. Therefore

$$F(r,p) \ge \frac{h\,(p\varepsilon_0 k)\,\tilde{g}(r_e) - g(r_e) r_e}{M(r_2)}.$$

Since h is increasing and unbounded, there exists $p > 0$ such that $F(r,p) > 1$ for any $r \in (r_e, r_2)$. $\square$

Theorem 3.10. *i) If $\lambda^* \le m(r_c)$ then $(r_c, 0)$ is a global attractor, except for the half axis $r = 0, \psi \ge 0$, of the nonautonomous ordinary differential system (3.5).*

ii) If $\lambda^* > m(0)$ then all the solutions of this system are unbounded except those lying on the half axis $\psi = 0, r \ge 0$

iii) If $m(r_c) < \lambda^* < m(0)$, i.e., if System (3.7) has the coexistence equilibrium point (r_e, ψ_e) such that $0 < r_e < r_c$, $\lambda^* = m(r_e)$ and $\psi_e = f^{-1}\left(\frac{g(r_e) r_e}{\tilde{g}(r_e)}\right)$. Then we have

a) If $G'(r_e) > 0$ and the closed orbits of System (3.7) are all isolated, then any solution of (3.5), with initial conditions $(r_0, 1) \ne (r_e, \psi_e)$ such that $r_0 > 0$, tends to one of these periodic orbits.

b) Let us assume that $G'(r_e) < 0$. If System (3.7) has no periodic orbits, then the coexistence equilibrium point (r_e, ψ_e) is a global attractor of the solutions corresponding to the initial condition $(r_0, 1)$ with $r_0 > 0$. Otherwise, if the closed orbits of (3.7) are all isolated then (r_e, ψ_e) is the ω-limit of all the solutions of System (3.5) enclosed by the first closed orbit and any other solution such that $r_0 > 0$ tends to one of these periodic orbits.

c) Finally, if $\tilde{g}(r) = r$ then (r_e, ψ_e) is a global attractor except for the solutions (r, ψ) such that $r = 0$ or $\psi = 0$.

Proof. In the case ii) we have that ψ'/ψ is larger than a constant $k > 0$ and r' is negative from r_c onward, hence the result.

In the other cases the solutions are all bounded. Furthermore the autonomous ordinary differential system (3.7) has the global attractor $(r_c, 0)$ in the first case (see the discussion following Proposition 3.2) and (r_e, ψ_e) in the case a) of iii) (see Proposition 3.3). So, the proof in these cases is now straightforward using Theorem 3.8. Finally in the other cases of iii) the statements follow immediately from Corollary 3.2 and Theorem 3.8 and Theorem 3.9. $\square$

3.3.4 Asymptotic behaviour of the age dependent model

Once we have studied the dynamics of the asymptotically autonomous ordinary differential system (3.5), we will be interested in this section in the study of the asymptotic behaviour of the age dependent model (3.1). The clue is the form of the solution corresponding to the consumer population which is expressed as a product of the solution of the linear part of the first and the second equation of (3.1) and the scalar function which is the solution of the second equation of (3.5). This special form allows ourselves to easily determine the dynamics of (3.1) using the results of the previous section.

Namely, from the proof of Theorem 2.2 we have that $b = (\nu + \lambda^*)e^{\lambda^* l}$ and using Theorem 2.7 it follows that, in the case of the uniform increase of mortality, the steady states are $(0,0,0)$ and $(0,0,r_c)$ and $(\alpha\varphi, 0), \forall \alpha > 0$ if $\lambda^* = m(0)$ or $(c_0\varphi, r_e)$ where $c_0 > 0$ and $\frac{g(r_e)r_e}{\tilde{g}(r_e)} = h\left(c_0(L\varphi)\right)$ in the case that $m(r_e) = \lambda^*$ and $0 < r_e < r_c$.

Theorem 3.11. *i) If $\lambda^* \leq m(r_c)$ and $r_0 > 0$, then $(0,0,r_c)$ is a global attractor of the initial value problem (3.1)*

ii) If $\lambda^* > m(0)$ then all the solutions, except those starting from $(u_0, v_0) = (0,0)$, $r_0 \geq 0$, are unbounded.

iii) If there exists $0 < r_e < r_c$ such that $\lambda^* = m(r_e)$, then there is $c_0 > 0$ such that $\frac{g(r_e)r_e}{\tilde{g}(r_e)} = h(c_0 L\varphi)$. And it follows that

a) If $\frac{d}{dr} f^{-1}\left(\frac{g(r)r}{\tilde{g}(r)}\right)\Big|_{r=r_e} > 0$ and the closed orbits of System (3.7) are all isolated, then the ω-limit set of a solution of the age-dependent model (3.1) such that $(u_0, v_0) \neq (0,0)$, $r_0 > 0$ and $(u_0, v_0, r_0) \neq (c_0\varphi, r_e)$ is a periodic *orbit* $\left(\tilde{\psi}_p(t)\,\varphi, \tilde{r}_p(t)\right)$ *where* $\left(\tilde{r}_p(t), \tilde{\psi}_p(t)\right)$ *is a limit cycle of System (3.7) and* $\varphi(a) = \left(be^{-\lambda^* a}, 1\right)$ *is an eigenvector of the operator* A *associated to* λ^*.

b) *If* $\frac{d}{dr} f^{-1}\left(\frac{g(r)r}{\tilde{g}(r)}\right)\Big|_{r=r_e} < 0$ *and System (3.7) has no periodic orbit then the coexistence equilibrium point* $(c_0\varphi, r_e)$ *is a global attractor of the solutions corresponding to the initial condition* (u_0, v_0, r_0) *with* $r_0 > 0$,. *If the condition on the derivative holds and the closed orbits of (3.7) are all isolated then* $(c_0\varphi, r_e)$ *is the* ω*-limit of all the solutions of System (3.1) with initial condition* (u_0, v_0, r_0) *such that* $(r_0, 1)$ *is surrounded by the first closed orbit, and any other solution of this model such that* $(u_0, v_0) \neq (0, 0)$ *and* $r_0 > 0$ *tends to a periodic orbit* $(\psi_p(t)\,\varphi, r_p(t))$ *where* $(r_p(t), \psi_p(t))$ *is a limit cycle of System (3.7).*

c) *Finally, if* $\tilde{g}(r) = r$ *then* $(c_0\varphi, r_e)$ *is an attractor of the solutions of the initial value problem with initial conditions* (u_0, v_0, r_0) *such that* $(u_0, v_0) \neq (0, 0)$ *and* $r_0 > 0$.

Proof. We recall that the solutions of the initial value problem are given by the formula

$$(u(t), v(t), r(t)) = \left(\psi(t)e^{-\lambda^* t} S(t)(u_0, v_0), r(t)\right).$$

Then, in the case b) when there is no closed orbit of (3.7) and in the case c), Theorem (3.5) implies that the solution tends to $(\psi_e c(u_0, v_0)\varphi, r_e)$, as $t \to +\infty$, where

$$c(u_0, v_0) = \frac{v_0 + \int_0^a e^{-\lambda^*(l-s)} u_0(x)dx}{1 + ble^{-\lambda^* l}}.$$

Furthermore, using the definition of ψ_e and f we have $\frac{g(r_e)r_e}{\tilde{g}(r_e)} = f(\psi_e) = h\left(\psi_e c(u_0, v_0)L(\varphi)\right)$. As h is monotonous, and c_0 is such that $\frac{g(r_e)r_e}{\tilde{g}(r_e)} = h\left(c_0 L\varphi\right))$ then $\psi_e c(u_0, v_0) = c_0$, independently of the initial conditions. Finally, in the other cases, using Theorem 3.10, the proofs are now straightforward. □

Remark 3.4. *i) The case* $\lambda^* \leq m(r_c)$, *i.e.* $r_e \geq r_c$, *leads to the extinction of the predator because the carrying capacity* r_c *is less than or equal to the resource level needed for its persistence.*

i) In the cases where the closed orbits of the autonomous ordinary differential system (3.7) are not isolated, some $\omega-$limit set of a solution can be an union of periodic orbits (see [81]).

Chapter 4

Asymptotic Behaviour of the Initial Value Problem for a Semilinear Equation

In the previous chapter, the dynamics of the solutions of Problem (2.1) in the special case of uniforme increase of mortality was studied. Now, dropping out this condition, we turn our interest to the general case proposed in (2.1). We exploit the semilinear formulation of the initial value problem (2.1) to determine the asymptotic behaviour of the solutions in terms of the birth rate b, taken as a parameter (we note that in the case of uniform increase of mortality the asymptotic behaviour of the solutions depends directly on the real number λ^* which is the dominant eigenvalue of the operator A).

In the first section the stability/instability and the bifurcation of these equilibria are studied. The stability of the coexistence equilibrium point is only established near bifurcation (near the equilibrium $(0, 0, r_c)$). In Sect. 4.2, under slightly more restrictive hypotheses, the stability properties of the coexistence equilibrium are analyzed using characteristic equation. The loss of stability via a Hopf bifurcation leads to the existence of a periodic solution. Sect. 4.3 is devoted to proving existence of a compact global attractor which contains a coexistence equilibrium.

4.1 Stability and bifurcation of an equilibrium point

We start by studying instability and local stability of the non-coexistence equilibria. The following theorem deals with these issues. Denoting $M_1(a,r) := \int_0^a m_1(s,r)\,ds$, we have

Theorem 4.1. *The equilibrium point* $(0,0,0)$ *is unstable. Moreover, if* $b < m_2(0)e^{M_1(l,0)}$, *it is a saddle point with a one dimensional unstable manifold. On the other hand, if* $b < m_2(r_c)e^{M_1(l,r_c)}$ *then the equilibrium point* $(0,0,r_c)$ *is asymptotically stable and it is unstable if* $b > m_2(r_c)e^{M_1(l,r_c)}$.

Proof. Notice that, as System (2.1) is semilinear, the linearization principle holds (see [86]). Let us start by the linearization of System (2.1) at the point $(0,0,r_c)$. So let $u(a,t) = \overline{u}(a,t)$, $v(t) = \overline{v}(t)$ and $r(t) = r_c + \overline{r}(t)$. Using the Taylor expansion it follows

$$\begin{cases} \overline{u}_t + \overline{u}_a & = & -m_1(a, r_c + \overline{r})\overline{u}, \\ & = & -(m_1(a,r_c) + \frac{\partial m_1(a,r_c)}{\partial r}\overline{r} + \ldots)\overline{u}, \\ \overline{u}(0,t) & = & b\overline{v}(t), \\ \overline{v}' & = & \overline{u}(l,t) - (m_2(r_c) + m_2'(r_c)\overline{r} + \ldots)\overline{v}, \\ \overline{r}' & = & (g(r_c) + g'(r_c)\overline{r} + \ldots)(r_c + \overline{r}) + \ldots - (h'(0)L(\overline{u},\overline{v}) + \ldots)(\tilde{g}(r_c) + \\ & & \tilde{g}'(r_c)\overline{r} + \ldots). \end{cases}$$

So we have the linear system

$$\begin{cases} \overline{u}_t + \overline{u}_a & = & -m_1(a,r_c)\overline{u}, \\ \overline{u}(0,t) & = & b\overline{v}(t), \\ \overline{v}' & = & \overline{u}(l,t) - m_2(r_c)\overline{v}, \\ \overline{r}' & = & -\tilde{g}(r_c)h'(0)L(\overline{u},\overline{v}) + g'(r_c)r_c\overline{r}. \end{cases}$$

Now, taking $\overline{u}(a,t) = e^{\lambda t}u(a)$, $\overline{v}(t) = e^{\lambda t}v$ and $\overline{r}(t) = e^{\lambda t}r$, this last system will be transformed into

$$\begin{cases} u'(a) + m_1(a,r_c)u(a) & = & -\lambda u(a), \\ u(l) - m_2(r_c)v & = & \lambda v, \\ -\tilde{g}(r_c)h'(0)L(u,v) + g'(r_c)r_c r & = & \lambda r, \end{cases}$$

with the boundary condition $u(0) = bv$.

The left hand side of this system defines an operator $\tilde{B}$ with domain $D(B)$. $\tilde{B}$ has a compact resolvent because for some λ, $(\lambda I - \tilde{B})^{-1}$ is a bounded operator from Y into $D(B)$ endowed with the norm $\|u\|_{W^{1,1}(0,l)} + |v| + |r|$ and $D(B)$ is compactly embedded in Y by Rellich's theorem (see [14]) because l is finite. Therefore the spectrum of $\tilde{B}$ reduces to the set of eigenvalues by the Riesz-Schauder Theory (see [30, VII.4.5]).

From the first equation we get $u(a) = bve^{-\lambda a - M_1(a,r_c)}$. If $v = 0$ then $u \equiv 0$ and $r \neq 0$ implies $\lambda = g'(r_c)r_c < 0$. Otherwise, from the second equation we obtain the characteristic equation $be^{-\lambda l - M_1(l,r_c)} - m_2(r_c) = \lambda$.

For $\lambda \in \mathbb{R}$ let us define $f(\lambda) := be^{-\lambda l - M_1(l,r_c)} - m_2(r_c)$. $f(\lambda)$ has a unique fixed point $\lambda(b)$ which is bigger than $-m_2(r_c)$ and it is negative if and only if $b < m_2(r_c)e^{M_1(l,r_c)}$ and it is positive if $b > m_2(r_c)e^{M_1(l,r_c)}$, which gives instability in this case. For $\lambda = x + iy, y \neq 0$, the real part of the characteristic equation is $be^{-xl - M_1(l,r_c)} \cos yl - m_2(r_c) = x$. So, $x \leq -m_2(r_c)$ if $\cos yl \leq 0$. If $0 < \cos yl < 1$ then $0 < b \cos yl < b$ and it is easy to see that $x < \lambda(b)$. Finally, $\cos yl$ cannot be 1 because then $\sin yl = 0$, and the imaginary part of the characteristic equation would imply $y = 0$. So the hypothesis $b < m_2(r_c)e^{M_1(l,r_c)}$ implies that the equilibrium point $(0, 0, r_c)$ is asymptotically stable.

The linear part at $(0, 0, 0)$ has $(0, 0, 1)$ as an eigenvector corresponding to the eigenvalue $g(0) > 0$. A computation similar to the previous one shows that $(0, 0, 1)$ is the only unstable eigenvector whenever $b < m_2(0)e^{M_1(l,0)}$. □

Corollary 4.1. *If $b < m_2(0)e^{M_1(l,0)}$ and $r_0 = 0$ then $u(t)$ and $v(t)$ tend to 0 as t goes to infinity.*

Proof. The linear manifold $r_0 = 0$ is invariant for the solutions of (2.1); System (2.1) becomes linear on this invariant subspace and under the hypothesis $b < m_2(0)e^{M_1(l,0)}$, all the eigenvalues have a negative real part. □

Remark 4.1. *If $b > m_2(0)e^{M_1(l,0)}$ the solutions are unbounded even with $r = 0$. This situation is obviously lacking any biological sense.*

Now we deal with the global dynamics of the solutions of (2.1), assuming that the death rate of juveniles, which will be denoted by $m_1(r)$, depends only on the amount of resources. In order to do this, we study the dynamics of the whole consumer population $p(t) + v(t)$ where $p(t) := \int_0^l u(a,t)da$ is the young population number.

Notice that, integrating the first equation of Problem (2.1), we obtain, assuming smoothness of the solutions of (2.1),

$$p'(t) = u(0,t) - u(l,t) - \int_0^l m_1(a, r(t))u(a,t)\, da$$

. Then

$$(p+v)'(t) = -\int_0^l m_1(a, r(t))u(a,t)\, da - (m_2(r(t)) - b)\, v(t). \tag{4.1}$$

Let us now prove the same relation for mild solutions of (2.1).

Proposition 4.1. *Let $(u(t), v(t), r(t))$ be a mild solution of Problem (2.1) corresponding to any initial condition $(u_0, v_0, r_0) \in Y^+$. Then the function $(p+v)(t)$ is of class C^1 in $[0,\infty)$ and (4.1) holds for its derivative.*

Proof. Applying the operator N defined in Theorem 2.3 to the first two components of (2.6), we have

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

Applying Theorem 2.3, differentiating under the integral and using (2.6) we obtain

$$\begin{aligned}
(p+v)'(t) &= bS_2(t)\begin{pmatrix} u_0 \\ v_0 \end{pmatrix} - m_1(a, r(t))p(t) - m_2(r(t))v(t) \\
&\quad -b\int_0^t S_2(t-s)\begin{pmatrix} m_1(a, r(s))u(s) \\ m_2(r(s))v(s) \end{pmatrix} ds \\
&= -m_1(a, r(t))p(t) - m_2(r(t))v(t) - bv(t). \quad \square
\end{aligned}$$

Now, we state the following technical lemma

Lemma 4.1. *Let (u, v, r) be a solution of Problem (2.1) such that $u(a,t) \geq 0, v(t) \geq 0$ and $r(t) > 0$ for all $a \in [0,l]$ and $t \geq 0$. Let us assume that the functions u and v tend to 0 in X as t goes to ∞. If the function $r(t)$ has also a limit at infinity then* $\lim_{t\to\infty} r(t) = r_c$.

Proof. First, the function $r(t)$ satisfies the following integral equation

$$r(t+1) - r(t) = \int_t^{t+1} g(r(s))r(s) - h\,(L(u(s), v(s)))\,\tilde{g}(r(s))ds.$$

It is clear that $h(L(u(t), v(t))) \longrightarrow 0$ as t goes to infinity and from the previous integral equation it follows that $g(r(t))r(t) \longrightarrow 0$. So as $t \longrightarrow +\infty$ we have $r(t) \longrightarrow 0$ or $g(r(t)) \longrightarrow 0$. Let assume that $r(t) \longrightarrow 0$, so for all $0 < \varepsilon < r_c$ there exists $T > 0$ and $\alpha > 0$ such that if $t > T$ then $0 < r(t) < \varepsilon, \tilde{g}(r(t)) < \alpha r(t)$, because $\tilde{g}$ is a smooth increasing function vanishing at 0, and $h(L(u(t), v(t))) < g(\varepsilon)/2\alpha$. So, for $t > T$ it follows

$$r'(t) = g(r(t))r(t) - h(L(u(t), v(t)))\,\tilde{g}(r(t)) > \left(g(\varepsilon) - \frac{g(\varepsilon)}{2}\right) r(t) > 0.$$

In conclusion, $r(t)$ does not tend to 0 and, therefore $g(r(t)) \longrightarrow +\infty$, i.e. the limit of $r(t)$ has to be r_c. $\square$

The following is a first result on global asymptotic behaviour that will be completed in Section 4.3 using more general methods.

Theorem 4.2. *If $b \leq m_2(\infty)$ then $(0, 0, r_c)$ is a global attractor for Problem (2.1) except for the solutions with initial value such that $r_0 = 0$, which tend to the origin.*

If $b \in (m_2(\infty), m_2(r_c))$ then the solutions with initial condition $r_0 > 0$ such that $b < m_2(r_0)$ tend to $(0, 0, r_c)$, too.

Proof. Assume $b \leq m_2(\infty)$. Then, $(0, 0, 0)$ and $(0, 0, r_c)$ are the only equilibrium points of Problem (2.1). From (4.1) and using $m_1(a, r) > \mu > 0$ for $a \in [0, l], r \geq 0$, $(p + v)'(t) \leq -\min(\mu, m_2(r(t)) - b))\,(p + v)(t)$ which implies that $(p + v)(t) \leq (p + v)(0)e^{-Kt}$ where $K := \min(\mu, m_2(\max(r_0, r_c)) - b) > 0$. Here we used the fact that the third equation in (2.1) implies that $r(t) \leq \max(r_0, r_c)$ and therefore $m_2(r(t)) - b \geq m_2(\max(r_0, r_c)) - b$, which is positive by hypothesis. So $p(t)$ and $v(t)$ tend to 0 as $t \longrightarrow \infty$. In particular, $u(t)$ tends to 0 in $L^1[0, l]$ as $t \longrightarrow \infty$.

For $u(t)$ and $v(t)$ given and tending to 0, the third equation in (2.1) is asymptotically autonomous and its solutions $r(t)$ are bounded. The limit equation $r' = g(r)r$ has r_c as a global attractor of the positive solutions. Now we use Theorem 3.7 and Theorem 3.8 (see [59, 81]) and we will have that the $\omega-$limit set of the forward bounded solution $r(t)$ is $\omega(r) = \{r_c\}$ or $\omega(r) = \{0\}$. By Lemma 4.1, the $\omega-$limit set of a positive $r(t)$ cannot reduce to 0. So $r(t)$ tends to r_c. $\square$

We end Section 4.1 with the study of the bifurcation at the equilibrium point $(0, 0, r_c)$ and we start by stating the following perturbation results which will be used in the proof of Theorem 4.5. These results are presented respectively as Lemma 1.3 of [20] and as Theorem 3.17 of [48].

Theorem 4.3. *(Crandall and Rabinowitz) Let X and Y be Banach spaces such that $X \subset Y$ and the embedding I is continuous. Let T_0 be a bounded linear map of X into Y and assume that r_0 is a simple real eigenvalue of T_0. Then there exists $\delta > 0$ such that whenever T is a bounded linear map of X into Y and $\|T - T_0\| < \delta$, there exists a unique $r(T) \in \mathbb{R}$ satisfying $|r(T) - r_0| < \delta$ for which $T - r(T)I$ is singular.*

Notice also that the following theorem will be the principle result used the study of the perturbation of (2.1) in the next chapter.

Theorem 4.4. *(T. Kato) Let T be a closed operator in a Banach space X and let B be an operator in X which is T-bounded, i.e., such that $D(T) \subset D(B)$ and*

$$\|Bu\| \leq c\|u\| + d\|Tu\|, u \in D(T),$$

where c, d are nonnegative constants. If there is a point λ of the resolvent set of T such that

$$c\|(T - \lambda)^{-1}\| + d\|T(T - \lambda)^{-1}\| < 1,$$

then $S = T + B$ is closed and λ belongs to the resolvent set of S.

Theorem 4.5. *There exists $\varepsilon > 0$ such that if*

$$m_2(r_c)e^{M_1(l,r)} < b < m_2(r_c)e^{M_1(l,r_c)} + \varepsilon < m_2(0)e^{M_1(l,0)},$$

where $M_1(a, r) := \int_0^a m(s, r)\, ds$, then there exists an asymptotically stable equilibrium branches off from $(0, 0, r_c)$ as $b = b_0 := m_2(r_c)e^{M_1(l,r_c)}$.

Proof. In order to use the results on bifurcation theory contained in Lemma 1.1, Corollary 1.13 and Theorem 1.16 by Crandall and Rabinowitz in [20] we translate the equilibrium point $(0, 0, r_c)$ to the origin of coordinates and we rewrite the equilibrium problem (2.9) as $F(b, x) = (0, 0, 0)$ where F is defined, for $b > 0$ and $x = (u, w, r) \in \{(u, w) \in W^{1,1}[0, l] \times \mathbb{R}; u(0) = w\} \times \mathbb{R}$, as

$$F(b, x) :=$$
$$\left(-u_a - m_1(r_c + r)u\, ,\, u(l) - m_2(r_c + r)\tfrac{w}{b}\, ,\, \left(g(r_c + r) - h\left(L(u, \tfrac{w}{b})\right)\right)(r_c + r)\right),$$

taking values in Y.

We have $F(b,0)=(0,0,0)$ for all $b>0$ and from the proof of Theorem 4.1 it follows that 0 is an algebraically simple eigenvalue of $T_0 := F_x(b_0,0)$ with associated eigenvector $x_0 = \left(e^{-M_1(a,r_c)}, 1, \tilde{r}_0\right)$, where $\tilde{r}_0 = \tilde{g}(r_c)h'(0)L\left(e^{-M_1(a,r_c)}, 1/b_0\right)/g'(r_c)r_c$. It is easy to see that

$$Range(T_0) = \{(f,\alpha,\beta)\in Y; \int_0^l e^{M_1(s,r_c)-M_1(a,r_c)} f(s)\,ds + \alpha = 0\},$$

and thus $x_0 \notin Range(T_0)$. The codimension of $Range(T_0)$ is 1 because it is the kernel of a nontrivial continuous linear form. Then there exist two continuously differentiable functions $b(s)$ and $\psi(s)$ defined in a neighbourhood of 0 and taking values in $\mathbb{R}$ and in a complement subspace of $span\{x_0\}$ in the domain of F, respectively, such that $b(0)=b_0, \psi(0)=0$ and $F(b(s),x(s))=0$ where $x(s)=sx_0+s\psi(s)$. Moreover $x(s)$ is the only nontrivial equilibrium near 0 for values of the parameter b close to b_0 (see Lemma 1.1 of [20]).

We recall that r denotes $r(s)$ the third component of $x(s)$. Note that $r'(0)=\tilde{r}_0$. Now let $\phi(r) := m_2(r_c+r)e^{M_1(l,r_c+r)}$. The equilibrium condition implies that $\phi(r(s)) = b(s)$. Taking derivatives at $s=0$ we get $\phi'(r(0))r'(0) = \phi'(r(0))\tilde{r}_0 = b'(0)$ and so as $\phi'(r(0))<0$ and $\tilde{r}_0<0$ then $b'(0)$ is positive.

Let us denote $\lambda(b)$ the dominant eigenvalue of $F_x(b,0)$, already dealt with in the proof of Theorem 4.1 as the dominant eigenvalue of the linear part of System (2.1) at the equilibrium point $(0,0,r_c)$. In particular $\lambda(b)<0$ if $b<b_0, \lambda(b_0)=0$ and $\lambda(b_0)>0$ if $b>b_0$. Moreover, the characteristic equation for $\lambda(b)$ is $\lambda(b) = be^{-(\lambda(b)l+M_1(l,r_c))} - m_2(r_c)$ (see the proof of Theorem 4.1). Taking implicit derivatives we get $\lambda'(b)>0$ for all $b>0$.

Let us denote $T = F_x(b(s),x(s))$. We shall prove that T has a dominant real eigenvalue $\mu(s)$ and $\mu(s)$ is negative when $s>0$, i.e. when $b(s)>b_0$.

We know that 0 is a simple eigenvalue of T_0 and that there exists a number $\omega>0$ such that $Re(\sigma(T_0)\setminus\{0\}) \subset (-\infty,-\omega)$. For any $\delta\in(0,\omega/2), (T_0-\lambda I)^{-1}$ is an analytic function on $C_\delta = \{\lambda\in\mathbb{C}; Re\lambda \geq -\omega/2, |\lambda|\geq\delta\}$. So $\|(T_0-\lambda I)^{-1}\|$ is a continuous function of λ on this closed set and tends to 0 at infinity. So there exists a constant k_δ such that $\|(T_0-\lambda I)^{-1}\| < k_\delta$. On the other hand, in view of the continuity of $F_x(b,x), b(s)$ and $x(s)$, for any $\delta>0$ there exists $\varepsilon>0$ such that $|s|<\varepsilon$ implies that $\|T-T_0\|<\delta$.

Finally, by Theorem 4.3 there exists $\delta_0, 0<\delta_0<\omega/2$ such that, if $\|T-T_0\|<\delta_0$

then there is a unique spectral value of T with modulus less than δ_0, $\mu(s)$, which is a real simple eigenvalue .

Let $|s|$ be so small that $\|T - T_0\| < \min(\delta_0, 1/k_{\delta_0})$ and let λ belong to C_{δ_0} and hence to the resolvent set of T_0. As $\|T - T_0\| \| (T_0 - \lambda I)^{-1} \| < 1$, from Theorem 4.4 (with $d = 0$) it follows that λ belongs to the resolvent set of T. Therefore, $\mu(s)$ is a dominant eigenvalue of T and by the linear stability principle, the stability of $x(s)$ depends on the sign of $\mu(s)$. From [20, Theorem 1.16] we have

$$\lim_{\substack{s \to 0 \\ \mu(s) \neq 0}} \frac{-sb'(s)\lambda'(b_0)}{\mu(s)} = 1,$$

and hence $\mu(s) < 0$ for s positive, sufficiently small.

Remark 4.2. *Obviously the bifurcating branch is made up of the equilibrium* (u_e, v_e, r_e) *given by Theorem 2.7.*

4.2 Change of stability of the coexistence equilibrium point via Hopf bifurcations

For the sake of simplicity and in order to perform some explicit computations related to the stability properties of the equilibrium, we will assume in the rest of Chap. 4 (and Chap. 6) that m_1 depends only on the resource level r.

4.2.1 Linearization and characteristic equations

The purpose of this subsection is to study the possible loss of stability of the coexistence equilibrium solution (u_e, v_e, r_e) of (2.1). This occurs only when the first eigenvalue of the characteristic equation, obtained from the linearization of Problem (2.1) at this coexistence equilibrium point, crosses the imaginary axis. This can generate a Hopf bifurcation of periodic solutions (see [25, Chap. X, Theorem 2.7] and [41]). Our stability analysis will rest on inspection, using linearisation theory, of the eigenvalues (roots of the characteristic equations of the linearizations). So let $u(a,t) = u_e + \overline{u}(a,t)$, $v(t) = v_e + \overline{v}(t)$ and $r(t) = r_e + \overline{r}(t)$. Using Taylor expansion it follows, from Problem (2.1),

$$\begin{cases} \overline{u}_t + \overline{u}_a + \frac{\partial u_e}{\partial a} &=& -(m_1(r_e) + m_1'(r_e)\overline{r} + \ldots)(u_e + \overline{u}), \\ \overline{u}(0,t) &=& b\overline{v}(t), \\ \overline{v}' &=& u_e(l) + \overline{u}(l,t) - (m_2(r_e) + m_2'(r_e)\overline{r} + \ldots)(v_e + \overline{v}), \\ \overline{r}' &=& (g(r_e) + g'(r_e)\overline{r} + \ldots - h(L(u_e,v_e)) - h'(L(u_e,v_e))L(\overline{u},\overline{v}) \\ & & - \ldots)(r_e + \overline{r}). \end{cases}$$

which leads to the following linear system (dropping the nonlinear terms)

$$\begin{cases} \overline{u}_t + \overline{u}_a &=& -m_1(r_e)u(a) - m_1'(r_e)\overline{r}u_e(a), \\ \overline{u}(0,t) &=& b\overline{v}(t), \\ \overline{v}' &=& \overline{u}(l,t) - m_2(r_e)\overline{v} - m_2'(r_e)v_e\overline{r}, \\ \overline{r}' &=& g'(r_e)r_e\overline{r} - r_e h'(L(u_e,v_e))L(\overline{u},\overline{v}). \end{cases} \tag{4.2}$$

Finally, setting $\overline{u}(a,t) = e^{\lambda t}u(a)$, $\overline{v}(t) = e^{\lambda t}v$ and $\overline{r}(t) = e^{\lambda t}r$, the eigenvalue problem associated with (4.2) reads

$$\begin{cases} -u'(a) - m_1(r_e)u(a) - m_1'(r_e)ru_e(a) &=& \lambda u(a), \\ u(l) - m_2(r_e)v - m_2'(r_e)v_e r &=& \lambda v, \\ g'(r_e)r_e r - r_e h'(L(u_e,v_e))L(u,v) &=& \lambda r, \\ u(0) &=& bv. \end{cases} \tag{4.3}$$

In order to simplify the notations, let us define $M_i := m_i(r_e)$ and $M_i' := m_i'(r_e)$ for $i = 1,2$. Let us also remind that for $i = 1,2$, M_i' are assumed to be negative throughout the work (see 2.2).

For $\lambda \in \mathbb{C}$ let us define $f(\lambda) := be^{-(M_1+\lambda)l} - M_2 - \lambda$ which may be written as $f(\lambda) = M_2(e^{-\lambda l} - 1) - \lambda$ because $b = M_2 e^{M_1 l}$.

The function $f(\lambda)$ has a unique real zero, $\lambda = 0$, which is not an eigenvalue of the linear system (4.3). Indeed, for $\lambda = 0$, the first and the last equations in (4.3) yield $u(a) = b(v - M_1' v_e r a)e^{-M_1 a}$ and, then, the second one gives $-M_1' M_2 v_e l r = M_2' v_e r$. As M_1' and M_2' are both negative, this implies $r = 0$. Finally, the third equation yields $u \equiv 0$ and $v = 0$ because h is strictly increasing and L is a strictly positive linear form.

For $\lambda = x + iy, y \neq 0$, the real part of the equation $f(\lambda) = 0$ is

$$M_2(e^{-xl}\cos(yl) - 1) = x. \tag{4.4}$$

Firstly, for $\cos yl = 0$, (4.4) yields $x = -M_2$. Now, notice that $\tilde{f}(x) := M_2(e^{-xl}\cos(yl) - 1)$ is continuous as a function of x. After, if $0 < \cos(yl) < 1$ then the function $\tilde{f}(x)$ is strictly decreasing, comes from $+\infty$ when $\omega = -\infty$ and goes to $-M_2$ as $\omega \to \infty$ and $\tilde{f}(0) = M_2(\cos(yl) - 1)$. On the other hand, if $\cos(yl) < 0$ then the function $\tilde{f}(x)$ is strictly increasing, comes from $-\infty$ when $\omega = -\infty$ and goes to $-M_2$ as $\omega \to \infty$. So, any x, satisfying (4.4), is strictly negative. Now, notice that $\cos yl$ cannot be 1 because then $\sin(yl) = 0$, and the imaginary part of the same equation would imply $y = 0$. So the real parts of the nonvanishing zeroes of the function f are strictly negative. Thus, as we are looking for eigenvalues with nonnegative real parts, we may assume $f(\lambda) \neq 0$ and $\lambda \neq 0$. Solving System (4.3) we find that the first equation and the boundary condition are equivalent to having

$$u(a) = bve^{-(M_1+\lambda)a} + \frac{M_1' b v_e r}{\lambda}\left(e^{-(M_1+\lambda)a} - e^{-M_1 a}\right) \tag{4.5}$$

which yields applying the second equation

$$v(be^{-(M_1+\lambda)l} - M_2 - \lambda) + \frac{M_1' b v_e r}{\lambda}\left(e^{-(M_1+\lambda)l} - e^{-M_1 l}\right) = 0.$$

Hence

$$\begin{aligned} v &= \frac{v_e r}{f(\lambda)}\left(\frac{M_1' M_2}{\lambda}(1 - e^{-\lambda l}) + M_2'\right) \\ &= \frac{v_e r}{\lambda f(\lambda)}\left(M_1'(M_2(1 - e^{-\lambda l}) + \lambda) + (M_2' - M_1')\lambda\right) \\ &= \frac{(M_2' - M_1')v_e r}{f(\lambda)} - \frac{M_1' v_e r}{\lambda}. \end{aligned} \tag{4.6}$$

After, substituting v in (4.5) by the last term of (4.6) it follows that

$$u(a) = \frac{b(M_2' - M_1')v_e r}{f(\lambda)} e^{-(M_1+\lambda)a} - \frac{M_1' b v_e r}{\lambda} e^{-M_1 a}. \tag{4.7}$$

Now if $M_1' = M_2'$ holds then $v = \frac{-M_1' v_e r}{\lambda}$ and $u(a) = \frac{-M_1' u_e(a) r}{\lambda}$. So from the third equation of System (4.3) we have

$$\lambda^2 - g'(r_e)r_e\lambda - M_1' r_e h'(L(u_e, v_e))L(u_e, v_e) = 0.$$

The roots of this characteristic equation are

$$\lambda = \frac{g'(r_e)r_e}{2} \pm \frac{\sqrt{(g'(r_e)r_e)^2 + 4M_1' r_e h'(L(u_e, v_e))L(u_e, v_e)}}{2}.$$

In the right hand of this equality, the first term is always strictly negative and its absolute value is bigger than the second term. Hence, $Re\lambda < 0$. The following result is now obvious. $\square$

Theorem 4.6. *If $b \in \left(m_2(r_c)e^{m_1(r_c)l}, m_2(0)e^{m_1(0)l}\right)$ and $m_1'(r_e) = m_2'(r_e)$ then the unique coexistence equilibrium point (u_e, v_e, r_e) of System (2.1) is asymptotically stable.*

Now we deal with the case where $m_1'(r_e) \neq m_2'(r_e)$. Notice that in this case it is impossible to extract λ from $L(u,v)$ in the third equation of (4.3). This fact makes more difficult the analysis of the sign of the real parts of the eigenvalues of System (4.3). To overcome this difficulty we will assume in the forthcoming a somehow special form for operator L, namely, $L(u,v) := \int_0^l u(a)\, da + v$. Notice that with this choice, $L(u,v)$ is the total predator population density. Consequently, we have

$$L(be^{-(M_1+\lambda)a}, 1) = b\frac{1-e^{-(M_1+\lambda)l}}{M_1+\lambda} + 1 = bf_1(M_1+\lambda) + 1$$

and

$$L(u_e, v_e) = v_e(bf_1(M_1) + 1)$$

where $f_1(\lambda) := \frac{1-e^{-\lambda l}}{\lambda}$. After, using (4.5) and (4.6), a tedious computation leads to

$$\begin{aligned}
L(u,v) &= -\frac{M_1' r}{\lambda} L(u_e, v_e) + \frac{(M_2' - M_1')v_e r}{f(\lambda)} L(be^{-(M_1+\lambda)a}, 1) \\
&= -\frac{M_1' v_e r}{\lambda}(bf_1(M_1)+1) + \frac{(M_2'-M_1')v_e r}{-\lambda(M_2 f_1(\lambda)+1)}(bf_1(M_1+\lambda)+1) \\
&= -\frac{v_e r}{\lambda}\left(\left(bf_1(M_1) + 1 - \frac{bf_1(M_1+\lambda)+1}{M_2 f_1(\lambda)+1}\right)M_1' + \frac{bf_1(M_1+\lambda)+1}{M_2 f_1(\lambda)+1}M_2'\right) \\
&= \frac{-v_e r}{\lambda}\left(a_1(\lambda)M_1' + a_2(\lambda)M_2'\right)
\end{aligned}$$

where $a_2(\lambda) := \frac{bf_1(M_1+\lambda)+1}{M_2 f_1(\lambda)+1}$ and $a_1(\lambda) := bf_1(M_1) + 1 - a_2(\lambda)$. Taking $\alpha := g'(r_e)r_e (< 0)$ and $\beta := r_e h'(L(u_e, v_e)) (> 0)$, the third equation of (4.3) yields, for $\lambda \neq 0$, the following characteristic equation

$$\alpha + \beta\frac{v_e r}{\lambda}\left(a_1(\lambda)M_1' + a_2(\lambda)M_2'\right) = \lambda$$

which may be transformed in

$$\lambda = v_e\beta\left(\frac{a_1(\lambda)}{\lambda-\alpha}M_1' + \frac{a_2(\lambda)}{\lambda-\alpha}M_2'\right). \tag{4.8}$$

4.2.2 Stability and instability regions

We will use an idea borrowed from [41], in a similar context, namely that Equation (4.8) is linear in M_1' and M_2'. So, setting $\lambda = \gamma + i\omega$, it can be written as

$$\begin{pmatrix} \gamma \\ \omega \end{pmatrix} = J(\gamma, \omega) \begin{pmatrix} M_1' \\ M_2' \end{pmatrix} \tag{4.9}$$

where

$$J(\gamma, \omega) := v_e \beta \left(\begin{array}{cc} Re\left(\frac{a_1(\lambda)}{\lambda - \alpha}\right) & Re\left(\frac{a_2(\lambda)}{\lambda - \alpha}\right) \\ Im\left(\frac{a_1(\lambda)}{\lambda - \alpha}\right) & Im\left(\frac{a_2(\lambda)}{\lambda - \alpha}\right) \end{array} \right)$$

is a 2×2 real matrix.

As parameters vary, roots of (4.8) may cross the imaginary axis in the complex plane. The first of the roots of (4.8) (i.e. a root with a largest real part) crosses the imaginary axis is associated with loss of stability of the coexistence equilibrium point (u_e, v_e, r_e) of (2.1). This corresponds to a Hopf bifurcation of periodic solutions if the eigenvalue enters into the right half complex plane with nonzero speed (see [25], Chap. X, Theorem 2.7 and [41]). The imaginary part ω of the first eigenvalue which crosses the imaginary axis corresponds to the frequency of the periodic cycle near the bifurcation point, and the period of the cycle is given by $2\pi/\omega$.

Let us fix $\gamma = 0$ in order to locate the boundaries in the parameter space along which a Hopf bifurcation may occur. Then Equation (4.9) becomes

$$J(0, \omega) \begin{pmatrix} M_1' \\ M_2' \end{pmatrix} = \begin{pmatrix} 0 \\ \omega \end{pmatrix}. \tag{4.10}$$

With the exception of isolated values of ω for which $\det(J(0, \omega)) = 0$, we obtain M_1' and M_2' as functions of ω by

$$\begin{pmatrix} M_1' \\ M_2' \end{pmatrix} = J(0, \omega)^{-1} \begin{pmatrix} 0 \\ \omega \end{pmatrix}. \tag{4.11}$$

This gives curves in the plane (M_1', M_2'), parameterized by ω, along which Hopf bifurcations may occur (see [25], Chap. X,Chap. XI and [41]).

Before studying in detail the stability and instability of the coexistence equilibrium solution (u_e, v_e, r_e) of (2.1) we will give a global result, Theorem 4.7, whose proof is based on the following lemma

Lemma 4.2. *There exists $C < 0$ such that $|a_2(\lambda)|$ is bounded in the half plane $Re(\lambda) > C$.*

Proof. Firstly, it is clear that $|bf_1(M_1 + \lambda) + 1| = |\frac{b(1-e^{-(M_1+\lambda)l})}{M_1+\lambda} + 1|$ is bounded if $Re(\lambda) > -M_1/2$. For any $K \in \mathbb{R}$, if $Re(\lambda) > K$, the denominator of $a_2(\lambda)$ tends to 1 as $|\lambda| \longrightarrow \infty$. So, it suffices to prove that there exists $C \in [-\frac{M_1}{2}, 0)$ such that if $Re(\lambda) > C$ then $M_2 f_1(\lambda) + 1 \neq 0$.

Now notice that $\lim_{\lambda \to 0} M_2 f_1(\lambda) + 1 = M_2 l + 1 \neq 0$. On the other hand, for $\lambda \neq 0$, $M_2 f_1(\lambda) + 1 = 0$ is equivalent to $e^{-l\lambda} = 1 + \frac{\lambda}{M_2}$ which has no real nonzero solutions. Moreover, for any nonreal solution λ, $e^{-\lambda l}$ is nonreal too and one has

$$1 + \frac{Re(\lambda)}{M_2} = Re(e^{-l\lambda}) < |e^{-l\lambda}| = e^{-lRe(\lambda)},$$

which implies $Re(\lambda) < 0$. For any solution with real part bigger than $-\frac{M_1}{2}$ one also has

$$\left|1 + \frac{\lambda}{M_2}\right| = |e^{-l\lambda}| = e^{-lRe(\lambda)} < |e^{-lM_1/2}|.$$

So, the nonvanishing solutions with $Re(\lambda) > -\frac{M_1}{2}$ have negative real parts and form a finite set because a bounded set of zeros of an analytic function does not have accumulation points. Therefore, the statement follows taking C bigger than the maximum of the real parts of these solutions, or simply $-\frac{M_1}{2}$ if the set of solutions with $Re(\lambda) > -\frac{M_1}{2}$ is empty. □

The characteristic equation (4.8) can also be written in the form

$$\lambda(\lambda - \alpha) - v_e \beta (bf_1(M_1) + 1) M_1' = (M_2' - M_1') a_2(\lambda). \tag{4.12}$$

Let us fix all the parameters appearing in (4.12) but M_2'. As we have already noted, if $M_1' = M_2'$ the two solutions of (4.12) have negative real parts.

Let us now show that a solution of (4.12) in the open right half-plane can only appear by a crossing of the imaginary axis. Indeed, let us assume, for instance, that (there exists)

$$x_0 := \inf\{x > M_1' : (4.12) \text{ with } M_2' = x \text{ has a solution with a positive real part}\}.$$

Then there exists a decreasing sequence x_n tending to x_0 and a sequence λ_n of solutions of (4.12) corresponding to $M_2' = x_n$, all of them with positive real parts. λ_n

is a bounded sequence since the half left side of (4.12) is a polynomial whereas the right hand side is bounded in the right half plane by Lemma 4.2. Hence λ_n has a subsequence converging to a solution λ_0 of (4.12) corresponding to $M_2' = x_0$. Finally, $Re(\lambda_0)$ has to vanish because, otherwise, Rouché's theorem implies the existence of a solution of (4.12) in a neighborhood of λ_0 (so, with positive real part) for M_2' sufficiently close to and less than x_0 (see [22], [56, Chap. 5, Sect. 4] and [74]). This is in contradiction with the fact that x_0 is the infimum. Obviously, analogous arguments work if we change inf by sup or the roles of M_1' and M_2'.

Let Q be the set of the points in the open third quadrant of the plane (M_1', M_2') such that do not belong to the set $\{(M_1'(\omega), M_2'(\omega)) : \omega > 0\}$, image of the curve defined by (4.11). Notice that Q contains the half line $M_1' = M_2' < 0$ as it has been shown just above the statement of Theorem 4.6. Applying now Theorem 4.6, the following result is straightforward

Theorem 4.7. *Let us assume $L(u,v) := \int_0^l u(a)\ da + v$. Whenever the point $(m_1'(r_e), m_2'(r_e))$ belongs to the open connected component of Q containing the half line $M_1' = M_2' < 0$, the coexistence equilibrium solution (u_e, v_e, r_e) is asymptotically stable.*

Now we go into a more detailed analysis of the stability curves. Algebraic simplification in (4.11) yields

$$\begin{pmatrix} M_1'(\omega) \\ M_2'(\omega) \end{pmatrix} = \frac{(\omega^2+\alpha^2)\omega}{v_e\beta(bf_1(M_1)+1)Im(a_2(i\omega))} \left(\begin{array}{c} -Re\left(\frac{a_2(i\omega)}{-\alpha+i\omega}\right) \\ Re\left(\frac{a_1(i\omega)}{-\alpha+i\omega}\right) \end{array} \right).$$

On the other hand we have

$$\frac{a_2(i\omega)}{-\alpha+i\omega} = \frac{a_2(i\omega)}{\alpha^2+\omega^2}(-\alpha-i\omega)$$

and

$$\frac{a_1(i\omega)}{-\alpha+i\omega} = \frac{a_1(i\omega)}{\alpha^2+\omega^2}(-\alpha-i\omega).$$

So it follows that

$$Re\left(\frac{a_2(i\omega)}{i\omega-\alpha}\right) = \frac{-\alpha Re(a_2(i\omega)) + \omega Im(a_2(i\omega))}{\alpha^2+\omega^2}$$

and

$$Re\left(\frac{a_1(i\omega)}{i\omega-\alpha}\right)=\frac{-\alpha(bf_1(M_1)+1)+\alpha Re(a_2(i\omega))-\omega Im(a_2(i\omega))}{\alpha^2+\omega^2}.$$

Hence,

$$\begin{pmatrix}M_1'(\omega)\\M_2'(\omega)\end{pmatrix}=\frac{\omega}{v_e\beta(bf_1(M_1)+1)Im(a_2(\omega i))}M(\omega) \tag{4.13}$$

where

$$M(\omega):=\begin{pmatrix}\alpha Re(a_2(i\omega))-\omega Im(a_2(i\omega))\\-\alpha(bf_1(M_1)+1)+\alpha Re(a_2(i\omega))-\omega Im(a_2(i\omega))\end{pmatrix}.$$

The signs of $M_1'(\omega)$ and $M_2'(\omega)$ neither depend on v_e nor on β, since these are both positive. Without loss of generality, let us also set $l=1$. Now let us calculate the limit of $\binom{M_1'(\omega)}{M_2'(\omega)}$ as ω goes to 0. Firstly, it is clear that $a_2(0)=\frac{bf_1(M_1)+1}{M_2l+1}$. Thus, $Im(a_2(0))=0$. So, applying Hospital rule it follows that

$$lim_{\omega\to0}\frac{\omega}{Im(a_2(\omega))}=lim_{\omega\to0}\frac{i\omega}{iIm(a_2(\omega))}=\frac{-i}{(Im(a_2))'(0)}=\frac{1}{Re(a_2'(0))}.$$

Hence,

$$\begin{aligned}\lim_{\omega\to0}\begin{pmatrix}M_1'(\omega)\\M_2'(\omega)\end{pmatrix}&=\frac{1}{v_e\beta(bf_1(M_1)+1)Re(a_2'(0))}\begin{pmatrix}\alpha\frac{bf_1(M_1)+1}{M_2l+1}\\-\alpha(bf_1(M_1)+1)+\alpha\frac{bf_1(M_1)+1}{M_2l+1}\end{pmatrix}\\&=\frac{\alpha}{v_e\beta Re(a_2'(0))(M_2l+1)}\begin{pmatrix}1\\-M_2l\end{pmatrix}.\end{aligned}$$

After, it is easy to see that

$$\begin{aligned}a_2'(0)&=\frac{b}{M_2l+1}\frac{(1-M_1f_1(M_1))(1+lM_1)-1}{M_1^2}+\frac{(bf_1(M_1)+1)M_2}{(M_2l+1)^2}\frac{l^2}{2}\\&=\frac{1}{M_2l+1}\left(\frac{M_2(1+lM_1)-b}{M_1^2}+\frac{bf_1(M_1)M_2+M_2}{M_2l+1}\frac{l^2}{2}\right).\end{aligned}$$

Now, a tedious, but not complicated, computation gives

$$\lim_{\omega\to0}\begin{pmatrix}M_1'(\omega)\\M_2'(\omega)\end{pmatrix}=\frac{\alpha M_1^2}{v_e\beta L_1(M_1,M_2)}\begin{pmatrix}1\\-M_2\end{pmatrix} \tag{4.14}$$

where

$$L_1(M_1,M_2):=M_2\left(1+M_1+\frac{M_1^2}{2}-e^{M_1}+\frac{M_2M_1}{2(M_2+1)}(e^{M_1}-1-M_1)\right).$$

This implies that the curves (M_1', M_2'), parameterized by $\omega > 0$, start in the second or in the fourth quadrant depending on the sign of $L_1(M_1, M_2)$. On the other hand, let us remember that they cannot cross the line $M_1' = M_2'$. As, by biological reasons we are only admitting negative M_i', Hopf bifurcation may occur only when these curves go into the third quadrant.

As the important parameters are reduced to α, M_1 and M_2 (besides of M_1' and M_2'), whereas v_e and β play lesser roles, we denote $\Phi_{\alpha,M_1,M_2}(\omega) := (M_1'(\omega), M_2'(\omega)), \omega > 0$.

Figure 4.1 gives an idea about where the parameters M_1 and M_2 lie when System (2.1) has a biological sense, i.e. if the birth rate b is not extremely large.

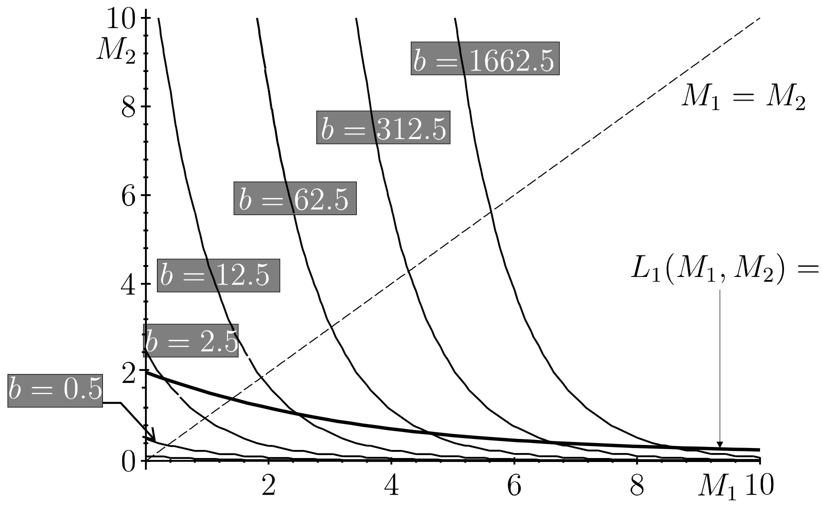

Figure 4.1: Level curves of the equilibrium condition $b = M_2 e^{M_1 l}$

Notice that if we take (M_1, M_2) such that $L_1(M_1, M_2) < 0$ then $\lim_{\omega\to 0} \Phi_{\alpha,M_1,M_2}(\omega)$ belongs to the fourth quadrant. On the other hand, $L_1(M_1, M_2) > 0$ implies that the curve $\Phi_{\alpha,M_1,M_2}(\omega)$ starts in the second quadrant. Finally, the points (M_1, M_2) satisfying $L_1(M_1, M_2) = 0$ are critical in the sense that the curve $\Phi_{\alpha,M_1,M_2}(\omega)$ comes from infinity.

Now we are interested in finding when the curve $\Phi_{\alpha,M_1,M_2}(\omega)$ goes into the third quadrant, i.e. to find values of the parameters for which Hopf bifurcation may occur. $M_1'(\omega) = 0$ holds if $\alpha Re(a_2(i\omega)) - \omega Im(a_2(i\omega)) = 0$, i.e. $\varphi_{M_1,M_2}(\omega) := \frac{\omega Im(a_2(i\omega))}{Re(a_2(i\omega))} = \alpha$ since $a_2(i\omega) \neq 0$ for all $\omega > 0$. We have $M_2'(\omega) = 0$ if $-\alpha(bf_1(M_1)+1)+\alpha Re(a_2(i\omega))-$

$\omega Im(a_2(i\omega)) = 0$, i.e. if $\psi_{M_1,M_2}(\omega) := \frac{\omega Im(a_2(i\omega))}{Re(a_2(i\omega))-bf_1(M_1)-1} = \alpha$(assuming $a_2(i\omega) \neq bf_1(M_1)+1$ for all $\omega \geq 0$).

$$\lim_{\omega\to\infty} \omega Im(a_2(i\omega)) = M_2 - b$$

The following lemmas, used in the proofs of Proposition 4.2 and Proposition 4.3, give the behaviour of the functions φ_{M_1,M_2} and ψ_{M_1,M_2} near 0 and near infinity. For intermediate values of ω the behaviour of these functions depends in a complicated way on (M_1, M_2). Numerical computations on this subject are presented in the last part of this section.

Lemma 4.3. *The following hold*

$$\begin{array}{rcl} \lim\limits_{\omega\to 0^+} a_2(i\omega) & = & \frac{bf_1(M_1)+1}{M_2+1}, \\ \lim\limits_{\omega\to 0^+} \dfrac{\varphi_{M_1,M_2}(\omega)}{\omega^2} & = & \dfrac{L_1(M_1,M_2)}{M_1^2(bf_1(M_1)+1)}, \\ \lim\limits_{\omega\to 0^+} \dfrac{\psi_{M_1,M_2}(\omega)}{\omega^2} & = & \dfrac{-L_1(M_1,M_2)}{M_2M_1^2(bf_1(M_1)+1)}. \end{array}$$

Proof. The first statement is obvious. The remaining ones follows directly from (4.13) and (4.14). $\square$

Lemma 4.4.

$$\begin{array}{rcl} \lim_{\omega\to\infty} a_2(i\omega) & = & 1, \\ \lim\limits_{\omega\to\infty} \varphi_{M_1,M_2}(\omega) & = & M_2 - b(<0), \\ \lim\limits_{\omega\to\infty} \psi_{M_1,M_2}(\omega) & = & \frac{b-M_2}{bf_1(M_1)}. \end{array}$$

Proof. It is very easy to show the first statement. For the second one, we have

$$\begin{array}{rcl} \omega a_2(i\omega) & = & \omega \dfrac{b\frac{1-e^{-M1}(\cos\omega - i\sin\omega)}{M_1+i\omega}+1}{M_2\frac{1-(\cos\omega-i\sin\omega)}{i\omega}+1} \\ & = & \dfrac{b+M_1-M_2\cos\omega+i(\omega+\sin\omega)}{M_2-M_2\cos\omega+i(\omega+\sin\omega)}\dfrac{i\omega^2}{M_1+i\omega}. \end{array}$$

On the other hand, at infinite, it follows that

$$\begin{aligned}\frac{b+M_1-M_2\cos\omega+i(\omega+\sin\omega)}{M_2-M_2\cos\omega+i(\omega+\sin\omega)} &= \frac{b+M_1-M_2\cos\omega+i(\omega+\sin\omega)}{(M_2-M_2\cos\omega)^2+(\omega+\sin\omega)^2} \\ &\quad (M_2-M_2\cos\omega-i(\omega+\sin\omega)) \\ &\simeq \frac{\omega^2+2\omega M_2\sin\omega}{(M_2-M_2\cos\omega)^2+(\omega+\sin\omega)^2} \\ &\quad +i\frac{b\omega-M_2\omega-M_1\omega}{(M_2-M_2\cos\omega)^2+(\omega+\sin\omega)^2}.\end{aligned}$$

and

$$\frac{i\omega^2}{M_1+i\omega}\simeq\omega+iM_1.$$

So,

$$\lim_{\omega\to\infty}\omega Im(a_2(i\omega))=\lim_{\omega\to\infty}\frac{(b-M_2)\omega}{(M_2-M_2\cos\omega)^2+(\omega+\sin\omega)^2}=M_2-b.$$

The rest follows from the definition of φ_{M_1,M_2} and ψ_{M_1,M_2}. □

Remark 4.3. *From the lemmas above it follows that the equalities*

$$0<Re(a_2(i\omega))<bf_1(M_1)+1 \tag{4.15}$$

hold for ω near 0 and near infinite. On the other hand, if (4.15) holds for all $\omega>0$ then the functions φ_{M_1,M_2} and ψ_{M_1,M_2} are continuous.

Proposition 4.2. *Let us assume that the hypothesis of Theorem 4.7 holds and that M_1 and M_2 be such that (4.15) holds for any $\omega>0$. Then there exists $\alpha_0<M_2-b<0$ such that for any $\alpha=g'(r_e)r_e<\alpha_0$, the coexistence equilibrium point (u_e,v_e,r_e) is asymptotically stable. In other words, the stability region, in the plane (M_1',M_2'), is the whole third open quadrant. Moreover, if $\alpha>\alpha_0$ then the instability region is non-empty.*

Proof. First notice that (4.15) implies that if there exists ω_0 such that $Im(a_2(i\omega_0))=0$ ($\Phi_{\alpha,M_1,M_2}(\omega)$ is unbounded in ω_0) then $M_1'(\omega)$ changes sign in ω_0 if and only if $M_2'(\omega)$ changes sign too. So, $\Phi_{\alpha,M_1,M_2}(\omega)$ goes into the third quadrant if and only if there exists ω_1 such that $M_1'(\omega_1)=0$ or $M_2'(\omega_1)=0$. Since $\varphi_{M_1,M_2}(\omega)$ and $\psi_{M_1,M_2}(\omega)$ are bounded, it suffices to take

$$\alpha_0=\min\left(\inf_{\omega\geq0}\varphi_{M_1,M_2}(\omega),\inf_{\omega\geq0}\psi_{M_1,M_2}(\omega)\right)$$

to avoid this possibility. □

Remark 4.4. *Notice that if $L_1(M_1, M_2) < 0$ then from Lemma 4.3 and Lemma 4.4 it follows that $Im(a_2(i\omega)) < 0$ for ω near 0 and near infinite. On the other hand, $L_1(M_1, M_2) > 0$ implies, using again Lemma 4.3 and Lemma 4.4, that $Im(a_2(i\omega)) = 0$ for some $\omega > 0$.*

Proposition 4.3. *Let us assume the hypothesis of Theorem 4.7 and that M_1 and M_2 be such that $L_1(M_1, M_2) < 0$ and $Im(a_2(i\omega)) < 0$ for any $\omega > 0$.Then for any $\alpha = g'(r_e)r_e < 0$ there exists $\varepsilon > 0$ such that $(M_2' =)m_2'(r_e) > -\varepsilon$ implies that (u_e, v_e, r_e) is asymptotically stable.*

Proof. The curve $\Phi_{\alpha,M_1,M_2}(\omega)$ is continuous since $Im(a_2(i\omega))$ does not vanish and it starts in the fourth quadrant because $L_1(M_1, M_2) < 0$. Moreover, this curve tends to infinite as $\omega \longrightarrow \infty$ and it does not cross the diagonal. So $\Phi_{\alpha,M_1,M_2}(\omega)$ lies at a strictly positive distance from the semiaxis $M_1' \leq 0$. □

Remark 4.5. *The pairs (M_1, M_2) biologically meaningful must lie under some level curve of the function $M_2 e^{M_1}$ corresponding to relatively small birth rate b. Some numerical computations (see Subsect. 4.2.3) indicate that the hypothesis (4.15) of Proposition (4.2) holds, for instance, if $M_2 e^{M_1} \leq 12.5$. Besides, in this case, the same numerical computations show that the first hypothesis of Proposition (4.3) (i.e., that $L_1(M_1, M_2) < 0$) implies the second one.*

4.2.3 Numerical results

The following table gives some values of the number α_0 appearing in Proposition (4.2) in function of the parameters M_1 and M_2

M_1	M_2	b	α_0
0.01	11.5	11.615	-0.35
0.01	12.5	12.625	-0.4
0.01	1.5	1.51	-.027
0.2	1.5	1.832	-0.46
0.2	4	4.885	-1.46
0.2	9.5	11.603	-4
0.5	0.5	0.824	-0.4
1	1	2.718	-1.84
1	4	10.873	-6.6
2	1	7.389	-6.5
3	0.5	10.042	-9.6

These computations indicate that $|\alpha_0|$ increases with both M_i.

Finally, we study in detail two particular cases. In the first one we will take $M_1 = M_2 = 1$, i.e. $L_1(M_1, M_2) < 0$ and $b = e$ and in the second one $M_1 = 0.5$, $M_2 = 7$, i.e. $L_1(M_1, M_2) > 0$ and $b = 11.54$.

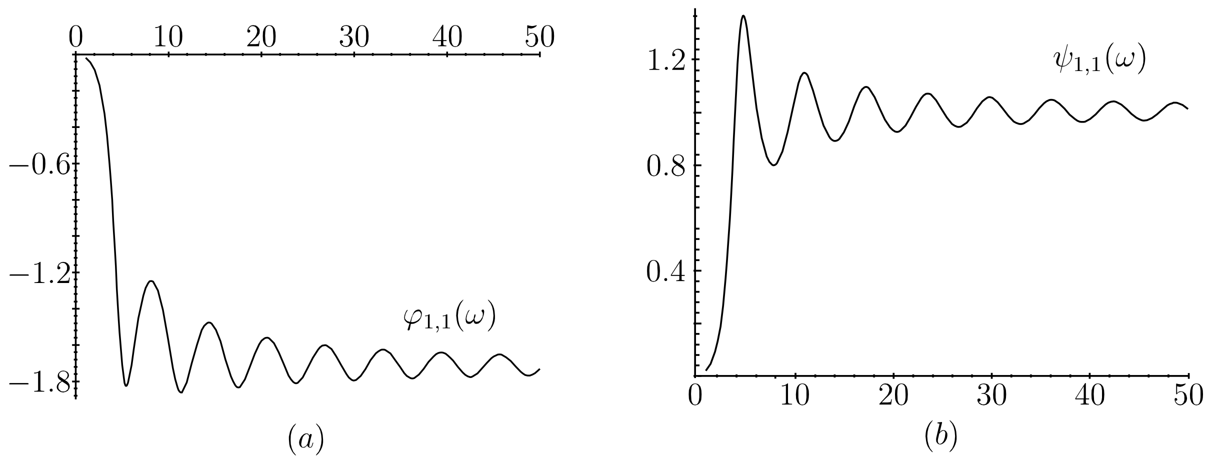

Figure 4.2: $M_1 = M_2 = 1$

Figure 4.2(a) shows that $\alpha_0 \simeq -1.84$ and that for any $\alpha < \alpha_0$, $\varphi_{M_1,M_2}(\omega) \neq \alpha$ for $\omega \geq 0$. So the curve $\Phi_{\alpha,1,1}(\omega)$ does not enter into the third quadrant and the coexistence equilibrium point (u_e, v_e, r_e) is asymptotically stable for any M_1' and M_2'.

On the other hand, Figure 4.2(a) also shows that if $\alpha_0 < \alpha$ then $\Phi_{\alpha,M_1,M_2}(\omega)$ crosses the vertical axis at least once. This means that (u_e, v_e, r_e) becomes unstable for some values of (M_1', M_2'). The curves shown in Figure 4.3 bound stability and instability regions of (u_e, v_e, r_e) for $\alpha = -1.6$ and for $\alpha = -0.5$, with $v_e = \beta = 1$ in both cases. Indeed, from (4.13) it follows that changing any of the parameters v_e or β only affects the norm of the curve $(M_1'(\omega), M_2'(\omega))$ i.e., only causes a change of scale.

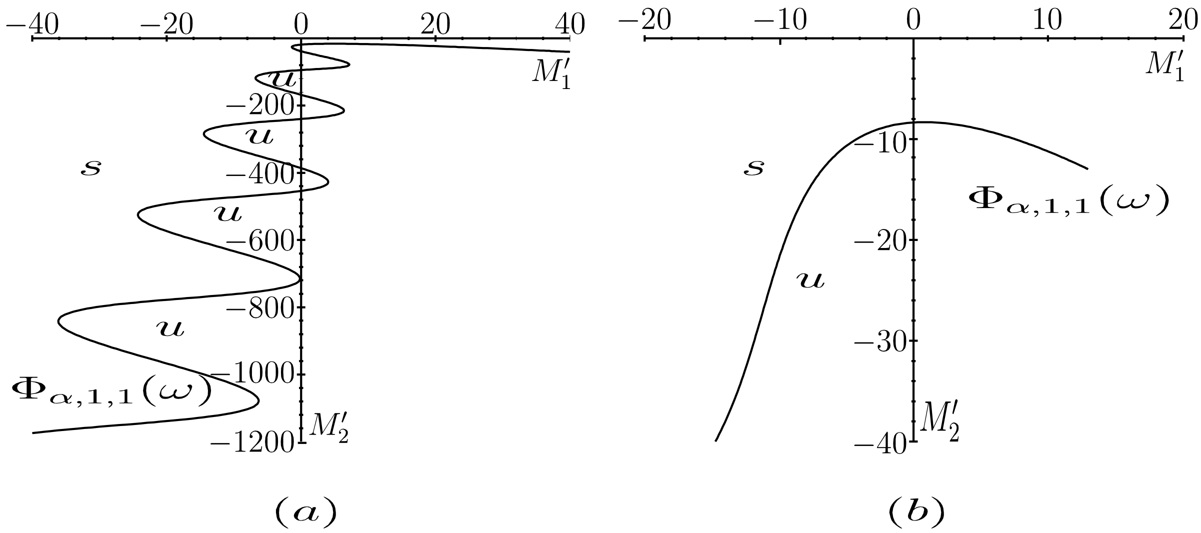

Figure 4.3: Curve $\Phi_{\alpha,1,1}(\omega)$: ($a$) with $\alpha = -1.6$; (b) with $\alpha = -0.5$

Now we deal with the case where $M_1 = 0.5$ and $M_2 = 7$.

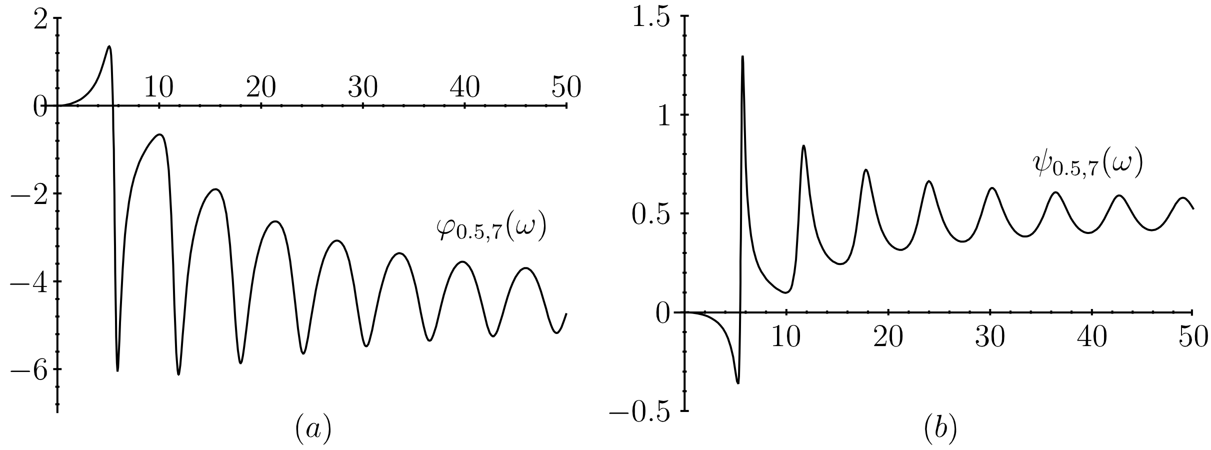

Figure 4.4: $M_1 = 0.5, M_2 = 7$

Figure 4.4 shows that we can take $\alpha_0 \simeq -6.2$. In Figure 4.5 the stability and instability regions for two choices of α are shown, taking again $v_e = \beta = 1$.

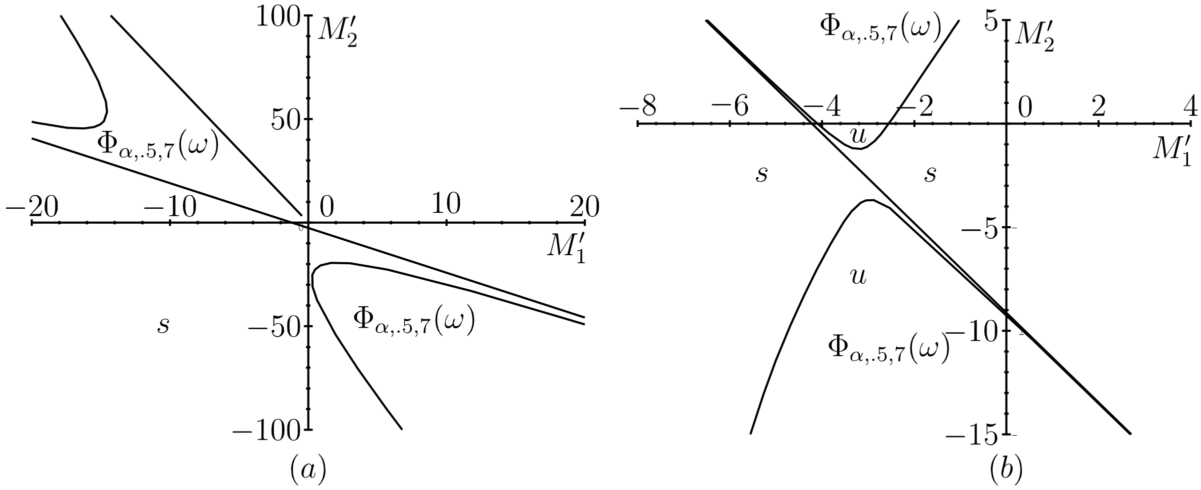

Figure 4.5: Function $\Phi_{\alpha,.5,7}(\omega)$: (a) with $\alpha = -6.5$; (b) with $\alpha = -0.2$

Remark 4.6. *It is very difficult to determine the sign of the derivative of the real part of the eigenvalues of (4.3) with respect to any parameter at any point of the curve* $\Phi_{\alpha,M_1,M_2}(\omega)$*. So, in the cases of Figure 4.3 and of Figure 4.5 the stability and instability regions have been determined by Theorem 4.7 and numerical computation of the roots of the characteristic equation 4.12.*

4.3 Existence of a global attractor

Sect. 4.1 and Sect. 4.2 were mainly devoted to local study near equilibrium points. This section deals with global dynamics when the mortality of the juveniles does not depend on the age, and although the complete asymptotic behaviour of the solutions of (2.1) cannot be elucidated by analytical means, the existence of a compact global attractor, and its description in some cases, is proven for most biologically significant situations.

As usual, the proof of the existence of such an attractor relies on two rather independent features of the nonlinear semigroup defined by the solutions of (2.1), namely, the property of asymptotic compactness and the existence of a fixed bounded set attracting every trajectory (i.e. the dissipativeness property).