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Oscillations in a system with material cycling*

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Abstract. We study a system of two integrodifferential equations which models the evolution of a biotic species feeding on an abiotic resource. We also consider nutrient recycling with time delay. By Hopf bifurcation theory we prove the existence of stable oscillations for a range of values of the input of nutrients.

Key words: Biotic species — Abiotic resource — Time delay — Stability — Hopf bifurcation

1. Introduction

Oscillatory behaviour of some planktonic algal communities is observed both in natural and laboratory systems (see e.g. Caperon 1969, and references therein). Caperon examined data obtained from a chemostat experiment with algae, and concluded that distributed delays must be considered in order to fit the experimental data. Also Waltman et al. (1980) suggest that the oscillations observed in a continuous culture of microorganisms may be due to the presence of time delays. In this paper we study a simple mathematical model with time lags describing the oscillatory behaviour of a biotic species feeding on an abiotic resource. We assume that the nutrient uptake rate is proportional to the nutrient concentration, according to the hypothesis that the nutrient considered is not abundant. The resource is a limiting nutrient, supplied at a constant rate. This situation can be easily reached into a laboratory system, and may approximate real systems during limited time intervals. Hsu et al. (1977) propose a model with a constant nutrient supply which describes the growth of phytoplanktonic communities in lakes during the summer months, when there is no nutrient circulation between the surface and the bottom of the water column. But during spring and fall the nutrient generated by the decomposition processes at the bottom can circulate and reach the algal communities living in the upper layers (Whittaker 1975).

Thus we insert into the model a term which takes into account the fact that a part of the dead biomass is recycled as a new resource; we refer to Anderson

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(1973) who proposes a computer simulation model with constant input of resource and recycling to describe the eutrophication of lakes. An instantaneous mathematical model of a closed system with material cycling was studied by Nisbet and Gurney (1976); they stress that time delays involved in the decomposition process cannot be neglected in boreal systems. Therefore we consider a time lag in the recycling term. We also consider a distributed time lag in the growth response to nutrition (D'Ancona 1954). We prove that such a model can have an unusual property in that its equilibrium is stable for low rates of nutrient supply, bifurcates towards stable oscillations when the supply is increased, then regains stability for larger values. It must be observed that the corresponding instantaneous model (Roy and Solimano 1986) has a globally stable equilibrium for each value of the parameters.

If we denote by N_1 the concentration of an abiotic resource and by N_2 the biomass of a biotic species, the evolution of our system is described by the following integrodifferential equations:

$$\begin{aligned} \dot{N}_1 &= R - a_{12}N_1N_2 + b_2e_2\int_{-\infty}^{t} \alpha\, e^{-\alpha(t-\tau)}N_2(\tau)\, d\tau \\ \dot{N}_2 &= N_2\left(-e_2 + \gamma_2\int_{-\infty}^{t} \beta\, e^{-\beta(t-\tau)}N_1(\tau)\, d\tau\right). \end{aligned} \tag{1.1}$$

where:

$R \in \mathbb{R}_+ := (0, +\infty)$ is the constant rate of nutrient supply,
$a_{12} \in \mathbb{R}_+$ is the coefficient of uptake of inorganic material,
$e_2 \in \mathbb{R}_+$ is the death rate coefficient for N_2,
$\gamma_2 \in \mathbb{R}_+$ is the coefficient of utilization of the nutrient,
$b_2 \in (0, 1)$ is the fraction of dead biomass which is recycled as a new nutrient.

We introduced distributed time lags because they are more realistic than discrete delays (see, e.g., Caswell 1972). However we agree with Hastings [8] who says that such terms should be viewed not as exact descriptions, but merely as a way of investigating the effects of including past history.

The integral term $\int_{-\infty}^{t} \beta\, e^{-\beta(t-\tau)}N_1(\tau)\, d\tau$ says that the growth of the species depends on the past concentration of the nutrient and has a diminishing effect the further it goes back in the past. The term $\int_{-\infty}^{t} \alpha\, e^{-\alpha(t-\tau)}N_2(\tau)\, d\tau$ takes account of the time lag due to the decomposition process by which a part of the dead biomass is introduced as a new resource. Exponential kernels are also used by Cunningham and Nisbet (1980), whereas Caperon [2] proposes non-increasing kernels in order to fit his experimental data. We observe that both the exponential delay kernels are normalized to one. According to MacDonald (1978) we define the average time lags as:

$$\bar{T}_\alpha = \int_0^\infty u\, e^{-\alpha u}\, du = \frac{1}{\alpha}; \qquad \bar{T}_\beta = \int_0^\infty u\, e^{-\beta u}\, du = \frac{1}{\beta}. \tag{1.2}$$

In Sect. 2 we study the local stability of the positive equilibrium and state conditions for Hopf bifurcation, assuming R as a bifurcation parameter.

In Sect. 3 we study the attractivity of the bifurcating periodic orbits near the bifurcation values by applying the method published by Hassard et al. (1981) for unbounded-delay functional differential equations.

We prove that in the nonnegative orthant of the (α, β) plane a region exists such that two Hopf bifurcations occur as R varies: for a fixed set of parameters we find that increasing value of R give rise to a first bifurcation from a locally stable positive equilibrium toward stable periodic oscillations, and a second one from stable orbits toward a higher locally stable equilibrium.

In the nonnegative orthant of the (α, β) plane other two regions exist; one in which a single Hopf bifurcation occurs, for decreasing values of R, toward stable periodic oscillations, and a second region where the positive equilibrium is locally stable for each positive value of R. Finally, in Sect. 4 we discuss our results and emphasize the role of the recycling term with time lag in the first equation.

2. Local stability and Hopf bifurcation of the positive equilibrium

The autonomous integrodifferential system (1.1), subject to initial conditions

$$N_i(t) \equiv \phi_i(t), \qquad -\infty < t \leq t_0, \qquad t_0 \in (-\infty, +\infty) \tag{2.1}$$

where ϕ_i are (at least piece-wise) continuous positive and bounded initial functions, possesses a unique positive solution $N_i = N_i(t)$, $i = 1, 2$, extendible on $[t_0, +\infty)$, continuously dependent on parameters and initial data [e.g., Cushing 1977]. For the sake of simplicity from now on we choose $t_0 = 0$. By an equilibrium of (1.1) we mean a solution $N_i(t) \equiv N_i^*$, $i = 1, 2$, $t \in (-\infty, +\infty)$ for constants N_i^*, $i = 1, 2$. System (1.1) admits the unique equilibrium

$$N^* = (N_1^*, N_2^*) = \left(\frac{e_2}{\gamma_2}, \frac{R}{e_2(a_{12}/\gamma_2 - b_2)}\right) \tag{2.2}$$

which is positive provided that

$$a_{12} > b_2 \gamma_2, \tag{2.3}$$

which we assume is true.

In this section we study the qualitative dynamic behaviour around the positive equilibrium of system (1.1) as the constant rate of nutrient supply R ranges in $\mathbb{R}_+$.

We follow the usual linearization procedure defining $x_i = N_i - N_i^*$, $i = 1, 2$, and substituting it into (1.1). By the further transformation $\tau = t + s$, we get the following form of (1.1):

$$\dot{x} = Lx + \int_{-\infty}^{0} K(s) x(t+s)\, ds + f(x) \tag{2.4}$$

where $x \in \mathbb{R}^2$

$$L = \begin{pmatrix} -a_{12} N_2^* & -a_{12} N_1^* \\ 0 & 0 \end{pmatrix}, \qquad K(s) = \begin{pmatrix} 0 & b_2\, e_2 \alpha\, e^{\alpha s} \\ N_2^* \gamma_2 \beta\, e^{\beta s} & 0 \end{pmatrix},$$

$$f = \begin{pmatrix} -a_{12} x_1 x_2 \\ \gamma_2 x_2 \int_{-\infty}^{0} \beta\, e^{\beta s} x_1(t+s)\, ds \end{pmatrix}. \tag{2.5}$$

Note that L is a constant real matrix and that delayed terms occur both in the linear and nonlinear parts of (2.4) and $f(x)$ is of a higher order in x. Clearly the instability or the asymptotic stability of the zero solution $x \equiv 0$ of (2.4) is equivalent to that of N^* as solution of (1.1).

The question whether the asymptotic stability of the zero solution of (2.4) is ensured by that of the zero solution of the linearized system

$$\dot{x} = Lx + \int_{-\infty}^{0} K(s)x(t+s)\, ds \tag{2.6}$$

has an affirmative answer since $f(x)$ is of higher order in x and in some open region around $x \equiv 0$ where $|x_1| < \delta$, $\delta > 0$ we have

$$\left| \int_{-\infty}^{0} \beta\, e^{\beta s} x_1(t+s)\, ds \right| < \delta \text{ for all } t \in [0, +\infty).$$

The linearized system (2.6) is asymptotically stable if and only if (e.g. Cushing 1977)

$$D(\lambda) := \det\left[\lambda I - L - \int_{-\infty}^{0} K(s)\, e^{\lambda s}\, ds\right] \neq 0 \text{ when } \operatorname{Re} \lambda \geq 0 \tag{2.7}$$

and this implies the local asymptotic stability of the zero solution of (2.4). $D(\lambda) = 0$ is called "characteristic equation" of (2.6) and in our case has the form:

$$D(\lambda) = \det\begin{pmatrix} \lambda + a_{12}N_2^* & a_{12}N_1^* - b_2 e_2 \int_{-\infty}^{0} \alpha\, e^{(\alpha+\lambda)s}\, ds \\ -N_2^* \gamma_2 \int_{-\infty}^{0} \beta\, e^{(\beta+\lambda)s}\, ds & \lambda \end{pmatrix} = 0 \tag{2.8}$$

Because of the particular delay-kernels we used, the characteristic equation (2.8) assumes the form of the fourth degree polynomial:

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0, \tag{2.9}$$

with the real coefficients a_i, $i = 1, \ldots, 4$ given by:

$$\begin{aligned} a_1 &= \alpha + \beta + a_{12}N_2^*(R) \\ a_2 &= \alpha\beta + (\alpha+\beta)a_{12}N_2^*(R) \\ a_3 &= \beta a_{12}(\alpha + e_2)N_2^*(R) \\ a_4 &= \alpha\beta\gamma_2 R \end{aligned} \tag{2.10}$$

We observe that all coefficients a_i in (2.10) are positive functions $a_i = a_i(R)$, $R \in (0, +\infty)$.

We further observe that the same characteristic equation can be obtained by the linear chain trick (MacDonald 1978) which gives an expanded system of four ordinary differential equations.

Because of the polynomial structure (2.9) with all the coefficients (2.10) real and positive, we use the Routh–Hurwitz criterion so that the asymptotic stability condition (2.7) holds true. Let $\psi : (0, +\infty) \to \mathbb{R}$ be the following continuously differentiable function of R:

$$\psi(R) := a_1(R)a_2(R)a_3(R) - a_3(R)^2 - a_4(R)a_1(R)^2. \tag{2.11}$$

Then an immediate consequence of the Routh–Hurwitz criteria is the following:

Theorem 2.1. *The equilibrium* N^* *of* (1.1) *is locally asymptotically stable if and only if* $\psi(R)>0$.

We also give a simple criterion, based on the function ψ, to study the occurrence of Hopf bifurcations of the positive equilibrium N^* as R varies in $\mathbb{R}_+$.

The assumptions for Hopf bifurcations occurring [7] are the usual ones, and require that the spectrum $\sigma(R)=\{\lambda|D(\lambda)=0\}$ of the characteristic equation is such that:

(2.i) there exists $R_0\in(0,+\infty)$ at which a pair of complex, simple eigenvalues $\lambda(R_0)$, $\bar{\lambda}(R_0)\in\sigma(R)$ are such that

$$\operatorname{Re}\lambda(R_0)=0, \qquad \operatorname{Im}\lambda(R_0):=\omega_0>0$$

and

$$\left.\frac{d\operatorname{Re}\lambda(R)}{dR}\right|_{R_0}\neq 0 \quad \text{(transversality condition);}$$

(2.ii) all other elements of $\sigma(R)$ have negative real parts. The criterion is given in the following theorem:

Theorem 2.2. *A Hopf bifurcation of the equilibrium* N^* *of* (1.1) *occurs at* $R=R_0\in(0,+\infty)$ *if and only if*

$$\psi(R_0)=0, \qquad \left.\frac{d\psi}{dR}\right|_{R_0}\neq 0. \tag{2.12}$$

Proof. Since the characteristic equation is the fourth degree polynomial (2.9) whose real coefficients are given in (2.10), denoted by λ_i $i=1,2,3,4$ its roots, then the following relations hold true:

$$\begin{aligned}\lambda_1+\lambda_2+\lambda_3+\lambda_4&=-a_1\\ \lambda_1\lambda_2+\lambda_1\lambda_3+\lambda_1\lambda_4+\lambda_2\lambda_3+\lambda_2\lambda_4+\lambda_3\lambda_4&=a_2\\ \lambda_1\lambda_2\lambda_3+\lambda_1\lambda_3\lambda_4+\lambda_2\lambda_3\lambda_4+\lambda_1\lambda_2\lambda_4&=-a_3\\ \lambda_1\lambda_2\lambda_3\lambda_4&=a_4\end{aligned} \tag{2.13}$$

Let us prove the necessity part of the theorem.

If for some $R_0\in(0,+\infty)$ a pair of complex simple eigenvalues exist, say $\lambda_1(R_0)=\bar{\lambda}_2(R_0)$, such that $\operatorname{Re}\lambda_1(R_0)=0$, then by substitution in (2.13) we obtain:

$$\begin{aligned}\lambda_3+\lambda_4&=-a_1\\ \omega_0^2+\lambda_3\lambda_4&=a_2\\ \omega_0^2(\lambda_3+\lambda_4)&=-a_3\\ \omega_0^2\lambda_3\lambda_4&=a_4\end{aligned} \tag{2.14}$$

where $\omega_0=\operatorname{Im}\lambda_1(R_0)$. Then combining together the first and third of (2.14) we obtain:

$$\omega_0^2=\frac{a_3}{a_1} \tag{2.15}$$

and by substitution in the last of (2.14) we finally get $\lambda_3\lambda_4 = a_4 a_1/a_3$. Then, the second equation of (2.14) offers

$$\psi(R_0) = a_1(R_0)a_2(R_0)a_3(R_0) - a_3(R_0)^2 - a_1^2(R_0)a_4(R_0) = 0 \qquad (2.16)$$

thus proving the first part of the necessity implication. If we write the characteristic equation (2.9) as $D(R, \lambda) = 0$, from the hypothesis it follows that $D(R_0, i\omega_0) = 0$. From (2.9) and the positivity of a_i, $i = 1, \ldots, 4$, it is easy to see that $\partial D/\partial\lambda\,|_{R_0, i\omega_0} \neq 0$. Then by the implicit function theorem:

$$\left.\frac{d\lambda_1}{dR}\right|_{R_0, i\omega_0} = -\left.\frac{\partial D}{\partial R}\right|_{R_0, i\omega_0} \Big/ \left.\frac{\partial D}{\partial \lambda}\right|_{R_0, i\omega_0}$$

whose real part is obtained after some simple calculations:

$$\left.\frac{d\,\mathrm{Re}\,\lambda_1}{dR}\right|_{R_0} = -\frac{a_1}{2(a_4a_1^2 + (a_1a_2 - 2a_3)^2)}\left.\frac{d\psi}{dR}\right|_{R_0} \qquad (2.17)$$

where $a_i := a_i(R_0)$, $i = 1, \ldots, 4$, and

$$\frac{d\psi}{dR} = \sum_{i=1}^{4} \frac{\partial\psi}{\partial a_i}\frac{da_i}{dR}. \qquad (2.18)$$

By (2.17) the assumption $d\,\mathrm{Re}\,\lambda_1/dR|_{R_0} \neq 0$ implies that $d\psi/dR|_{R_0} \neq 0$, and the necessity part of the proof is completed.

Let us prove the sufficiency part by assuming that (2.12) holds true.

Since $\psi(R_0) = 0$, from the Routh-Hurwitz criterion at least one root, say λ_1, of (2.9) has real part equal to zero. From the fourth of (2.13) it follows that $\mathrm{Im}(\lambda_1) = \omega_0 \neq 0$, and, since (2.9) has real coefficients, admits a root $\lambda_2 = \bar{\lambda}_1$. Since ψ is a continuous function of all its roots, λ_1 and λ_2 are complex conjugate for R in an open interval including R_0. If we denote by λ_3 and λ_4 the remaining roots, then (2.14) hold true. If λ_3 and λ_4 are complex conjugate, from the first of (2.14) it follows that $2\,\mathrm{Re}\,\lambda_3 = -a_1 < 0$; if λ_3 and λ_4 are real, from the first and the fourth of (2.14), it follows that $\lambda_3 < 0$ and $\lambda_4 < 0$. From (2.17) and from the assumption $d\psi/dR|_{R_0} \neq 0$, the transversality condition $d\,\mathrm{Re}\,\lambda_1(R)/dR|_{R_0} \neq 0$ follows. Then all the hypotheses of the Hopf bifurcation theorem are satisfied, and the proof is completed. □

In order to apply Theorem 2.1 and Theorem 2.2 it is suitable to give a more tractable structure of the function $\psi = \psi(R)$ in (2.11).

We define

$$D_2 = e_2\left(\frac{a_{12}}{\gamma_2} - b_2\right) \qquad (2.19a)$$

$$K = \frac{\alpha e_2(a_{12} - b_2\gamma_2)}{a_{12}(\alpha + e_2)} \qquad (2.19b)$$

and introduce the variable ξ defined as

$$\xi = \frac{a_{12}}{D_2}R, \qquad \xi \in \mathbb{R}_+. \qquad (2.20)$$

Then, the function $\psi(R)$ can now be seen as a function of the variable ξ:

$$\psi(\xi) = \beta(\alpha + e_2)\xi\phi(\xi) \tag{2.21}$$

where

$$\phi(\xi) = a\xi^2 + b\xi + c \tag{2.22}$$

and whose coefficients are given by:

$$\begin{aligned} a &= \alpha + \beta - K \\ b &= (\alpha + \beta)^2 - 2K(\alpha + \beta) - \beta e_2 \\ c &= (\alpha + \beta)[\alpha\beta - K(\alpha + \beta)] \end{aligned} \tag{2.23}$$

Because of the assumption (2.3), from (2.19) we can see that D_2, K are always positive and $K < \alpha$. So $a > 0$ whereas the sign of the cofficients b and c appears to be strongly dependent upon the parameters $(a, \beta) \in \mathbb{R}^2_+$, $\mathbb{R}^2_+ := \{(\alpha, \beta) \in \mathbb{R}^2 \mid \alpha > 0, \beta > 0\}$. By this reason, in the following of this section, we will restrict ourselves to study the sign of the function $\psi = \psi(\xi)$ as the parameters α, β vary in $\mathbb{R}^2_{+0}$ and the bifurcation parameter ranges in $\mathbb{R}_+$. Since $\xi \in \mathbb{R}_+$ and $(\alpha, \beta) \in \mathbb{R}^2_+$, from (2.21) it follows that $\psi(\xi) = 0$ if and only if $\phi(\xi) = 0$ and

$$\text{sign}\ \psi(R) = \text{sign}\ \psi(\xi) = \text{sign}\ \phi(\xi) \quad \text{for all } \xi \in \mathbb{R}_+ \tag{2.24}$$

Furthermore, if $\phi = \phi(\xi)$ vanishes at some $\xi = \xi_0 \in \mathbb{R}_+$, we have

$$\psi'(\xi_0) = \beta(\alpha + e_2)\phi(\xi_0) + \beta(\alpha + e_2)\xi_0\phi'(\xi_0) = \beta(\alpha + e_2)\xi_0\phi'(\xi_0).$$

Therefore

$$\text{sign}\ \psi'(\xi_0) = \text{sign}\ \phi'(\xi_0), \tag{2.25}$$

and from (2.20)

$$\text{sign}\ \psi'(\xi_0) = \text{sign}\ \psi'(R_0). \tag{2.26}$$

Furthermore, let $\lambda_1(R) = \bar{\lambda}_2(R)$ be the pair of simple complex and conjugate roots which bifurcate at R_0. Then because of (2.17) we can conclude that at each bifurcation point $R_0 \in \mathbb{R}_+$ the following holds true:

$$\text{sign} \left. \frac{d\ \text{Re}\ \lambda_1(R)}{dR} \right|_{R_0} = -\text{sign}\ \psi'(R_0). \tag{2.27}$$

From (2.24)-(2.27) it follows that we can derive the properties of $\psi(R)$ with respect to local asymptotic stability and Hopf bifurcation of the positive equilibrium (2.2) from the sign of $\phi(\xi)$ and $\phi'(\xi)$.

Since from (2.22) and (2.23) $\phi = \phi(\xi)$ is a parabola with positive coefficient a, we consider the following three cases:

(i) $c < 0$;
(ii) $c > 0$, $b < 0$ and $b^2 - 4ac > 0$;
(iii) $c > 0$ and $b > 0$, or $c > 0$, $b < 0$ and $b^2 - 4ac < 0$

Then the following corollaries of Theorem 2.1 and Theorem 2.2 hold:

Corollary 2.1. *In case* (i) *a unique Hopf bifurcation value* $R_0 \in \mathbb{R}_+$ *exists such that for all* $R \in (R_0, +\infty)$ *the positive equilibrium* N^* *is locally asymptotically stable.*

Proof. Since $c<0$, a unique $\xi_0 \in \mathbb{R}_+$ exists such that $\phi(\xi_0)=0$, $\phi'(\xi_0)>0$ and $\phi(\xi)>0$ if and only if $\xi \in (\xi_0, +\infty)$. Hence, because of (2.20), $R_0=(D_2/a_{12})\xi_0$ is the unique zero of $\psi(R)$ in $\mathbb{R}_+$ with $\psi'(R_0)>0$ and $\psi(R)>0$ if and only if $R \in (R_0, +\infty)$.

Corollary 2.2. *In case* (ii) *two values* $R_{01}, R_{02} \in \mathbb{R}_+$ *exist, say* $R_{01}<R_{02}$, *at each of which a Hopf bifurcation occurs. The positive equilibrium* N^* *is locally asymptotically stable for all* $R \in \mathbb{R}_+ - [R_{01}, R_{02}]$.

Proof. If the hypothesis (ii) holds, two distinct values ξ_{01} and ξ_{02} exist in $\mathbb{R}_+$, say $\xi_{01}<\xi_{02}$, such that $\phi(\xi_{01})=\phi(\xi_{02})=0$ with $\phi'(\xi_{01})<0$, $\phi'(\xi_{02})>0$, and $\phi(\xi)>0$ if and only if $\xi \in \mathbb{R}_+ - [\xi_{01}, \xi_{02}]$. Hence, because of (2.20), $R_{01}=(D_2/a_{12})\xi_{01}< R_{02}=(D_2/a_{12})\xi_{02}$ are the unique two zeros of $\psi(R)$ in $\mathbb{R}_+$ at which, thanks to (2.25), (2.26), $\psi'(R_{01})<0$ and $\psi'(R_{02})>0$. Furthermore $\psi(R)>0$ if and only if $R \in \mathbb{R}_+ - [R_{01}, R_{02}]$.

Corollary 2.3. *In case* (iii) *the equilibrium* N^* *is locally asymptotically stable for all* $R \in \mathbb{R}_+$.

Proof. Hypothesis (iii) ensures that $\phi(\xi)>0$ for all $\xi \in \mathbb{R}_+$ and therefore, from (2.20), (2.21) and Theorem 2.1 the thesis trivially follows. □

The conditions (i), (ii), (iii) select three complementary regions in the positive orthant of the (α, β) plane when considering *a*, *b*, *c* as functions of (a, β) according to (2.23). The situation is depicted in Fig. 1.

The most interesting region both from a biological and mathematical point of view, is region (ii). In fact in that region the average time lag $\bar{T}_\alpha = 1/\alpha$ of the decomposition process is greater than $\bar{T}_\beta = 1/\beta$ which is the average time lag of the nutrition process. Furthermore, as the nutrient supply parameter R varies within $\mathbb{R}_+$ two Hopf bifurcation values are met.

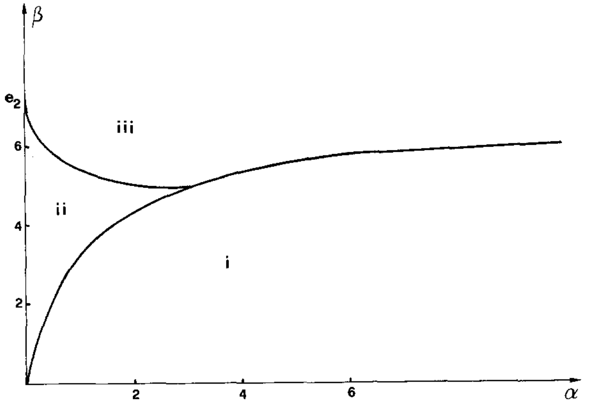

Fig. 1. Region (i) is bounded by the curve $\beta = \alpha e_2 F[\alpha + e_2(1-F)]$ (i.e. $c(\alpha, \beta)=0$), where $F=(a_{12}-b_2\gamma_2)/a_{12}$, and by the axis $\beta=0$. Region (ii) is bounded by the curves b^2-4ac, where *a*, *b*, *c* are defined in (2.23), and $c(\alpha,\beta)=0$ up to the tangency point (a, β) for which $b(\alpha,\beta)=0$, and by the axis $\alpha=0$. The curve $b^2-4ac=0$ is tangent to the ordinate axis for $\beta=e_2$. Region (iii) is the complement to the positive orthant of the union of region (i) and (ii). The curve $b^2-4ac=0$ results in a fourth degree algebraic equation of α and β. All the curves are plotted by a computer for the fixed set of the other parameters: $a_{12}=6$; $b_2=0.5$; $\gamma_2=2$; $e_2=7$

3. Stability of the bifurcating periodic solutions

In this section we investigate the system (2.4) to study the stability of the bifurcating closed orbits at the Hopf bifurcating parametric values provided by Corollary 2.1 and Corollary 2.2.

We follow the algorithm presented by [7] for delay-differential equations; another useful reference may be found in Stépán (1986), where the same kind of algorithm is followed by the author.

Let us transform (2.4) into the operator differential equation

$$\dot{x}_t = Ax_t + Fx_t \tag{3.1}$$

where $x = \mathrm{col}(x_1, x_2)$, $x_t(\theta) = x(t+\theta)$, $\theta \in (-\infty, 0]$. The linear operator A and the nonlinear one F are defined as follows:

$$A\phi(\theta) = \begin{cases} \dfrac{d\phi(\theta)}{d\theta} & -\infty < \theta < 0 \\ L\phi(0) + \int_{-\infty}^{0} K(s)\phi(s)\, ds & \theta = 0 \end{cases} \tag{3.2}$$

where the matrices L and $K(s)$ have already been defined in (2.5), and

$$F\phi(\theta) = \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix} & -\infty < \theta < 0 \\ \begin{pmatrix} -a_{12}\phi_1(0) \cdot \phi_2(0) \\ \gamma_2\phi_2(0) \int_{-\infty}^{0} \phi_1(s)\beta\, e^{\beta s}\, ds \end{pmatrix} & \theta = 0 \end{cases} \tag{3.3}$$

Note that both L and $K(s)$ depend upon the bifurcation parameter R through the equilibrium component $N_2^* = N_2^*(R)$ (see (2.2)). According to the usual nomenclature, we introduce as new bifurcation parameter

$$\mu := R - R_0, \qquad R, R_0 \in \mathbb{R}_+$$

such that the Hopf bifurcation occurs when $\mu = 0$. Obviously $A = A(\mu)$, but in most of the following computations, unless explicitly specified, it is implicitly assumed that $A = A(0)$. Note that A and its adjoint operator A^* can have complex eigenvectors. It is therefore suitable to allow for ϕ functions $\phi: (-\infty, 0] \to \mathbb{C}^2$ instead of $\mathbb{R}^2$.

The adjoint operator A^* is defined as follows:

$$A^*\psi(\delta) = \begin{cases} -\dfrac{d}{d\delta}\psi(\delta) & 0 < \delta < \infty \\ L'\psi(0) + \int_{-\infty}^{0} K'(s)\psi(-s)\, ds, & \delta = 0, \end{cases} \tag{3.4}$$

where L' and K' are transposted matrices and ψ: $[0, +\infty) \to \mathbb{C}^2$.

In order to determine the Poincaré normal form of operator A, we need to compute the eigenvector q of operator A belonging to the eigenvalue $i\omega_0$, and the eigenvector q^* of the adjoint operator A^* belonging to the eigenvalue $-i\omega_0$. We obtain:

$$q(\theta) = \begin{pmatrix} 1 \\ B \end{pmatrix} e^{i\omega_0\theta} \qquad -\infty < \theta \leq 0 \tag{3.5}$$

$$q^*(\theta) = D\begin{pmatrix} 1 \\ C \end{pmatrix} e^{i\omega_0\theta} \qquad 0 \leq \theta < \infty \tag{3.6}$$

where

$$B = -\frac{N_2^* \gamma_2 \beta}{\omega_0(\omega_0^2 + \beta^2)} (\omega_0 + i\beta) \tag{3.7}$$

$$C = \frac{a_{12} N_2^* \beta - \omega_0^2 - i\omega_0(\beta + a_{12} N_2^*)}{\beta \gamma_2 N_2^*} \tag{3.8}$$

and D is a free constant which must be determined by the condition

$$\langle q^*, q \rangle = 1, \tag{3.9}$$

where the scalar product $\langle .,. \rangle$ is defined as follows:

$$\langle \psi, \phi \rangle = \bar{\psi}'(0) \cdot \phi(0) + \int_{-\infty}^{0} \left(\int_{s}^{0} \bar{\psi}'(u-s) \cdot K(s) \phi(u) \, du \right) ds \tag{3.10}$$

Here $^-$ denotes the complex conjugate, and $\phi : (-\infty, 0] \to \mathbb{C}^2$, $\psi : [0, +\infty) \to \mathbb{C}^2$ are continuous and bounded functions.

If $\psi(0) = \mathrm{col}(\psi_1(0), \psi_2(0))$, $\phi(0) = \mathrm{col}(\phi_1(0), \phi_2(0))$, then by $\bar{\psi}'(0) \cdot \phi(0)$ we mean $\sum_{i=1}^{2} \bar{\psi}_i(0) \phi_i(0)$.

Hence, (3.9) with definition (3.10) gives:

$$\bar{D}\left(1 + B\bar{C} + \frac{\bar{C} N_2^* \gamma_2 \beta}{(\beta + i\omega_0)^2} + \frac{B b_2 e_2 \alpha}{(\alpha + i\omega_0)^2}\right) = 1 \tag{3.11}$$

from which the constant D can be easily obtained.

To construct the coordinates to describe the centre manifold $\mathscr{C}_0$ near the origin $x = 0$, let us consider the transformation:

$$z = \langle q^*, x_t \rangle, \qquad w = x_t - zq - \bar{z}\bar{q} \tag{3.12}$$

so that z and $\bar{z}$ are local coordinates for $\mathscr{C}_0$ in the directions of q and $\bar{q}$. In the variables z and w, (3.1) becomes:

$$\dot{z} = i\omega_0 z + \langle q^*(\theta), F(w + 2\,\mathrm{Re}\,\{zq(\theta)\}) \rangle \tag{3.13a}$$

$$\dot{w} = Aw - 2\,\mathrm{Re}\{\langle q^*(\theta), F(w + 2\,\mathrm{Re}\{zq(\theta)\}) \rangle q(\theta)\} + F(w + 2\,\mathrm{Re}\{zq(\theta)\}) \tag{3.13b}$$

On the manifold $\mathscr{C}_0$, $w(t, \theta) = w(z(t), \bar{z}(t), \theta)$ where

$$w(z, \bar{z}, \theta) = w_{20}(\theta) \frac{z^2}{2} + w_{11}(\theta) z\bar{z} + w_{02}(\theta) \frac{\bar{z}^2}{2} + \cdots \tag{3.14}$$

By the definition of the scalar product (3.10) and owing to (3.3) we may observe that

$$\langle q^*(\theta), F(w + 2\,\mathrm{Re}\{zq(\theta)\}) \rangle = q^*(0)' \cdot F(w(z, \bar{z}, 0) + 2\,\mathrm{Re}\{zq(0)\}) \tag{3.15}$$

Then according to Hassard et al. (1981), we define the functions

$$g(z, \bar{z}) := q^*(0)' \cdot F(w + 2\,\mathrm{Re}\{zq(0)\}) \tag{3.16}$$

$$H(z, \bar{z}, \theta) := F(w + 2\,\mathrm{Re}\{zq(\theta)\}) - 2\,\mathrm{Re}\{g(z, \bar{z}) q(\theta)\} \tag{3.17}$$

and we can rewrite (3.13a) and (3.13b) as:

$$\dot{z} = i\omega_0 z + g(z, \bar{z}) \tag{3.13a$'$}$$

$$\dot{w} = Aw + H(z, \bar{z}, \theta) \tag{3.13b$'$}$$

Our objective is to expand on $\mathscr{C}_0$ the function $g(z, \bar{z})$ in powers of z and $\bar{z}$:

$$g(z, \bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots \tag{3.18}$$

and to determine the coefficients of the expansion (3.18). This can be done by comparison of (3.18) with (3.16) when substituting for w its expansion (3.14). To compute the coefficients $w_{ij}(\theta)$ of (3.14), on $\mathscr{C}_0$ we expand the function $H(z, \bar{z}, \theta)$ in powers of $z, \bar{z}$:

$$H(z, \bar{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots \tag{3.19}$$

The coefficients of the expansion (3.19) can be computed from (3.17) as

$$H_{20} = \left[\frac{\partial^2}{\partial z^2}H\right]_{z=\bar{z}=0}, \qquad H_{11} = \left[\frac{\partial^2 H}{\partial z \partial \bar{z}}\right]_{z=\bar{z}=0},$$

i.e. (see Appendix 1):

$$H_{20}(\theta) = 2\bar{D}\Gamma q(\theta) + 2D\Gamma_1\bar{q}(\theta) + \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ 2\begin{pmatrix} -a_{12}B \\ \gamma_2\beta B(\beta - i\omega_0)/(\beta^2 + \omega_0^2) \end{pmatrix}, & \theta = 0 \end{cases} \tag{3.20}$$

with

$$\Gamma = a_{12}B - \bar{C}\frac{\gamma_2\beta B(\beta - i\omega_0)}{\beta^2 + \omega_0^2}; \qquad \Gamma_1 = a_{12}B - C\frac{\gamma_2\beta B(\beta - i\omega_0)}{\beta^2 + \omega_0^2}$$

$$H_{11}(\theta) = 2a_{12}(\mathrm{Re}\, B) \cdot (\bar{D}q(\theta) + D\bar{q}(\theta)) + \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ 2\begin{pmatrix} -a_{12}\,\mathrm{Re}\, B \\ 0 \end{pmatrix}, & \theta = 0 \end{cases} \tag{3.21}$$

On the other hand, near the origin, we write $w(z, \bar{z})$ as

$$\dot{w}(z, \bar{z}) = w_z\dot{z} + w_{\bar{z}}\dot{\bar{z}} \tag{3.22}$$

and using (3.14) to replace the derivatives w_z and $w_{\bar{z}}$ and (3.13a)$'$ to compute $\dot{z}$ and $\dot{\bar{z}}$, we get another expression for $\dot{w}$. Equating the right-hand side of (3.22) to that of (3.13b)$'$ with (3.19) we obtain:

$$(2i\omega_0 I - A)w_{20}(\theta) = H_{20}(\theta) \tag{3.23}$$

$$-Aw_{11}(\theta) = H_{11}(\theta) \tag{3.24}$$

and $w_{02} = \bar{w}_{20}$.

Following the procedure exposed in the Appendix 2 to solve (3.23), (3.24) we obtain:

$$w_{20}(\theta)=\mathrm{col}(w_{20}^{(1)}(\theta), w_{20}^{(2)}(\theta)), \qquad -\infty<\theta<0, \tag{3.25a}$$

where

$$\begin{aligned} w_{20}^{(1)}(\theta)&=\sigma_1\, e^{i\omega_0\theta}+\sigma_2\, e^{-i\omega_0\theta}+\sigma_f\, e^{2i\omega_0\theta}\\ w_{20}^{(2)}(\theta)&=\mu_1\, e^{i\omega_0\theta}+\mu_2\, e^{-i\omega_0\mu}+\mu_f\, e^{2i\omega_0\theta}\end{aligned} \tag{3.25b}$$

and

$$\sigma_1=-\frac{2\bar{D}\Gamma}{\omega_0}i; \qquad \sigma_2=-\frac{2D\Gamma_1}{3\omega_0}i; \qquad \mu_1=\sigma_1 B; \qquad \mu_2=\sigma_2\bar{B}. \tag{3.25c}$$

The free constants σ_f, μ_f are determined by the boundary conditions in $\theta=0$:

$$\sigma_f=w_{20}^{(1)}(0)-(\sigma_1+\sigma_2); \qquad \mu_f=w_{20}^{(2)}(0)-(\mu_1+\mu_2). \tag{3 25d}$$

Then we obtain:

$$w_{20}(0)=\mathrm{col}(w_{20}^{(1)}(0), w_{20}^{(2)}(0)) \tag{3.26a}$$

where

$$\begin{aligned} w_{20}^{(1)}(0)&=\frac{2i\omega_0 C_{20}^{(1)}-\left(a_{12}N_1^*-b_2e_2\alpha\dfrac{\alpha-2i\omega_0}{\alpha^2+4\omega_0^2}\right)C_{20}^{(2)}}{\Delta}\\ w_{20}^{(2)}(0)&=\frac{(2i\omega_0+a_{12}N_2^*)C_{20}^{(2)}+N_2^*\gamma_2\beta\dfrac{\beta-2i\omega_0}{\beta^2+4\omega_0^2}C_{20}^{(2)}}{\Delta}\end{aligned} \tag{3.26b}$$

and the expressions for $C_{20}^{(1)}$, $C_{20}^{(2)}$ and Δ are explicitly given in the Appendix 2. In the same manner we have:

$$w_{11}(\theta)=\mathrm{col}(w_{11}^{(1)}(\theta), w_{11}^{(2)}(\theta)), -\infty<\theta<0 \tag{3.27a}$$

where

$$\begin{aligned} w_{11}^{(1)}(\theta)&=\rho_1\, e^{i\omega_0\theta}+\rho_2\, e^{-i\omega_0\theta}+\rho_f\\ w_{11}^{(2)}(\theta)&=\chi_1\, e^{i\omega_0\theta}+\chi_2\, e^{-i\omega_0\theta}+\chi_f\end{aligned} \tag{3.27b}$$

and

$$\begin{aligned} \rho_1&=\frac{2a_{12}(\mathrm{Re}\, B)\bar{D}}{\omega_0}i; \qquad \rho_2=\bar{\rho}_1\\ \chi_1&=\rho_1 B; \qquad \chi_2=\rho_2\bar{B}.\end{aligned} \tag{3.27c}$$

The free constants ρ_f, χ_f are determined by the boundary conditions in $\theta=0$:

$$\rho_f=w_{11}^{(1)}(0)-(\rho_1+\rho_2); \qquad \chi_f=w_{11}^{(2)}(0)-(\chi_1+\chi_2) \tag{3.27d}$$

Then we obtain:

$$w_{11}(0)=\mathrm{col}(w_{11}^{(1)}(0), w_{11}^{(2)}(0)) \tag{3.28a}$$

with

$$w_{11}^{(1)}(0) = -\frac{C_{11}^{(2)}}{\gamma_2 N_2^*}, \qquad w_{11}^{(2)} = \frac{N_2^*(a_{12}C_{11}^{(2)} + \gamma_2 C_{11}^{(1)})}{\gamma_2 R_0}, \tag{3.28b}$$

where the expressions for $C_{11}^{(1)}$, $C_{11}^{(2)}$, are explicitly given in the Appendix 2. Now in (3.16) let us consider $F(w(z, \bar{z}, 0) + 2\,\mathrm{Re}\{zq(0)\})$. According to the definition (3.3) of operator F when $\theta = 0$, if we substitute for w its expansion (3.14), then we obtain the components of $F(w(z, \bar{z}, 0) + 2\,\mathrm{Re}\{zq(0)\})$ defined as:

$$f_0^1 := -a_{12}\left[(z+\bar{z}) + w_{20}^{(1)}(0)\frac{z^2}{2} + w_{11}^{(1)}(0)z\bar{z} + w_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right]$$
$$\times\left[(zB + \overline{zB}) + w_{20}^{(2)}(0)\frac{z^2}{2} + w_{11}^{(2)}(0)z\bar{z} + w_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right]. \tag{3.29}$$

$$f_0^2 := \gamma_2\left[(zB + \overline{zB}) + w_{20}^{(2)}(0)\frac{z^2}{2} + w_{11}^{(2)}(0)z\bar{z} + w_{02}^{(2)}(0)\frac{\bar{z}^2}{2}\right]$$
$$\times\left[z\frac{\beta(\beta - i\omega_0)}{\beta^2 + \omega_0^2} + \bar{z}\frac{\beta(\beta + i\omega_0)}{\beta^2 + \omega_0^2} + \tilde{w}_{20}^{(1)}\frac{z^2}{2} + z\bar{z}\tilde{w}_{11}^{(1)} + \frac{z^2}{2}\tilde{w}_{02}^{(1)}\right] \tag{3.30}$$

where:

$$\tilde{w}_{20}^{(1)} := \int_{-\infty}^{0} w_{20}^{(1)}(s)\beta\, e^{\beta s}\, ds; \qquad \tilde{w}_{11}^{(1)} := \int_{-\infty}^{0} w_{11}^{(1)}(s)\beta\, e^{\beta s}\, ds;$$
$$\tilde{w}_{02}^{(1)} := \int_{-\infty}^{0} w_{02}^{(1)}(s)\beta\, e^{\beta s}\, ds. \tag{3.31}$$

Thanks to (3.25b), (3.27b) the coefficients (3.31) can be explicitly computed (see Appendix 3), whereas the other coefficients $w_{ij}(0)$ occurring in (3.29), (3.30) are already given in (3.26b) and (3.28b).

Thus, according to the definition (3.16) of function $g(z, \bar{z})$ we finally obtain:

$$g(z, \bar{z}) = \bar{D}f_0^1 + \bar{D}\bar{C}f_0^2. \tag{3.32}$$

Now, if we equate the right hand side of (3.32) to that of (3.18), we obtain:

$$g_{20} = -2\bar{D}\Gamma \tag{3.33}$$

$$g_{11} = -2\bar{D}a_{12}\,\mathrm{Re}\,B \tag{3.34}$$

$$g_{02} = 2\bar{D}\bar{B}\left\{-a_{12} + \bar{C}\frac{\gamma_2\beta}{\beta^2 + \omega_0^2}(\beta + i\omega_0)\right\} \tag{3.35}$$

$$g_{21} = 2\bar{D}\left\{-a_{12}\left[\frac{\bar{B}w_{20}^{(1)}(0)}{2} + \frac{w_{20}^{(2)}(0)}{2} + w_{11}^{(1)}(0)B + w_{11}^{(2)}(0)\right]\right.$$
$$\left. + \bar{C}\gamma_2\left[\frac{\bar{B}\tilde{w}_{20}^{(1)}}{2} + \frac{w_{20}^{(2)}(0)\beta(\beta + i\omega_0)}{2(\beta^2 + \omega_0^2)} + \frac{w_{11}^{(2)}(0)\beta(\beta - i\omega_0)}{\beta^2 + \omega_0^2} + B\tilde{w}_{11}^{(1)}\right]\right\}. \tag{3.36}$$

Finally, thanks to (3.33)-(3.36), we can compute the complex number

$$C_1(0) = \frac{i}{2\omega_0}(g_{20}\cdot g_{11} - 2|g_{11}|^2 - \tfrac{1}{3}|g_{02}|^2) + \frac{g_{21}}{2}, \tag{3.37}$$

at the bifurcation value $\mu = 0$. Then we have (e.g.: Chap. 2: A Recipe-Summary, in Hassard et al. 1981):

$$\mu_2 = -\frac{\text{Re } C_1(0)}{\alpha'(0)}, \tag{3.38}$$

$$\tau_2 = -\frac{\text{Im } C_1(0) + \mu_2 \omega'(0)}{\omega_0}, \tag{3.39}$$

$$\beta_2 = 2 \text{ Re } C_1(0), \tag{3.40}$$

where

$$\alpha'(0) = \left.\frac{d \text{ Re } \lambda_1(R)}{dR}\right|_{R_0}, \qquad \omega'(0) = \left.\frac{d \text{ Im } \lambda_1(R)}{dR}\right|_{R_0}.$$

Provided that $\mu_2 \neq 0$, the kind of informations that we obtain from (3.38)-(3.40) is:

Theorem 3.1 (Hassard, Kazarinoff and Wan). *Let ε be a measure of the amplitude of a periodic solution $x_t = p_\varepsilon(t)$ of* (3.1)

$$\varepsilon := \max_t \|p_\varepsilon(t)\|. \tag{3.41}$$

Then, there is an open interval $(0, \varepsilon_1)$ *such that the open interval*

$$\mathcal{T}_1 = \left\{ \mu \,\middle|\, 0 < \frac{\mu}{\mu_2} < \frac{\mu(\epsilon_1)}{\mu_2} \right\} \tag{3.42}$$

has the following properties: for any μ in $\mathcal{T}_1$ there is a unique $\varepsilon \in (0, \varepsilon_1)$ for which $\mu(\varepsilon) = \mu$. Hence the family of periodic solutions $p_\varepsilon(t)$ $(0 < \varepsilon < \varepsilon_1)$ may be parametrized as $p(t; \mu)$, $\mu \in \mathcal{T}_1$. For $\mu \in \mathcal{T}_1$ the period $T(\mu)$ and the Floquet characteristic exponent $\beta(\mu)$ (here and in the following any confusion with the parameter β appearing in the exponential delay of nutrition process is to be avoided) are:

$$T(\mu) = \frac{2\pi}{\omega_0}(1 + \tau_2 \varepsilon^2 + 0(\varepsilon^4)) \tag{3.43}$$

$$\beta(\mu) = \beta_2 \varepsilon^2 + 0(\varepsilon^4) \tag{3.44}$$

where

$$\varepsilon^2 = \frac{\mu}{\mu_2} + 0(\mu^2), \qquad \mu := R - R_0. \tag{3.45}$$

The direction of the bifurcation is given by the sign of μ_2 in (3.38):

if $\mu_2 > 0$ then the bifurcating periodic solutions bifurcate from equilibrium for $R > R_0$; (3.46a)

if $\mu_2 < 0$ then the bifurcating periodic solutions bifurcate from equilibrium for $R < R_0$. (3.46b)

Furthermore

$$\text{sign } \beta(\mu) = \text{sign } \beta_2. \tag{3.47}$$

The periodic solutions $p(t, \mu)$ are orbitally asymptotically stable with asymptotic phase if $\beta_2 < 0$ and are unstable if $\beta_2 > 0$. As a comment to this theorem we may say that we are in the lucky situation in which we can easily determine the direction of the bifurcation.

In fact, in (2.27) we proved that

$$\operatorname{sign} \alpha'(0) = -\operatorname{sign}\left(\frac{d\psi(R)}{dR}\bigg|_{R_0}\right). \tag{3.48}$$

Since $\psi = \psi(R)$ is essentially a parabola with a positive second order coefficient, in the case (i) of Corollary 2.1, the unique zero of ψ and bifurcation point R_0 is crossed with $\psi'(R_0) > 0$ and therefore $\alpha'(0) < 0$.

The case (ii) is more interesting. In fact, by Corollary 2.2, $\psi = \psi(R)$ has two zero points $R_{01} < R_{02}$ the first which is crossed with $\psi'(R_{01}) < 0$ and the second with $\psi'(R_{02}) > 0$. Therefore $\alpha'(0)|_{R_{01}} > 0$ and $\alpha'(0)|_{R_{02}} < 0$.

Hence, we can give the following:

Lemma 3.2. *In case (i) one bifurcation point $R_0 \in \mathbb{R}_+$ exists at which*

$$\operatorname{sign}(\mu_2|_{R_0}) = \operatorname{sign}(\beta_2|_{R_0}); \tag{3.49}$$

In case (ii) two bifurcation points, say $R_{01} < R_{02}$, R_{01}, $R_{02} \in \mathbb{R}_+$, exist such that:

$$\operatorname{sign}(\mu_2|_{R_{01}}) = -\operatorname{sign}(\beta_2|_{R_{01}}); \qquad \operatorname{sign}(\mu_2|_{R_{02}}) = \operatorname{sign}(\beta_2|_{R_{02}}). \tag{3.50}$$

Now, with the same set of parameters $a_{12} = 6$, $b_2 = 0.5$, $\gamma_2 = 2$, $e_2 = 7$ already used in Fig. 1, we set up one pair of parameter values (α, β) in region (i), i.e.

(3.i) $\alpha = 2, \beta = 3$,

where, according to Corollary 2.1, one Hopf bifurcation value $R_0 \in \mathbb{R}_+$ exists. Then we set up another pair of parameter values (α, β) in region (ii), i.e.

(3.ii) $\alpha = \frac{1}{2}, \beta = 4$,

where, according to Corollary 2.2, two Hopf bifurcation values R_{01}, $R_{02} \in \mathbb{R}_+$ exist.

For both the sets of parameters (3.i) and (3.ii) we compute the complex number (3.37) and then we apply Theorem 3.1 and Lemma 3.2.

We obtain the following results:

(3.i) we have one Hopf bifurcation value at $R_0 = 7.77$. According to (3.37) and (3.40) we compute β_2 which results: $\beta_2 = -0.2254$. By Lemma 3.2 we know that $\operatorname{sign}(\mu_2|_{R_0}) = \operatorname{sign}(\beta_2|_{R_0}) < 0$. Therefore, by Theorem 3.1, the Hopf bifurcation occurs at $R < R_0$ toward orbitally asymptotically stable periodic solutions. By the (2.20) and (2.21) we can easily compute $d\psi/dR|_{R_0}$ and then, from (2.17) we obtain

$$\alpha'(0) = \frac{d \operatorname{Re} \lambda_1(R)}{dR}\bigg|_{R_0}.$$

Hence from (3.38) and (3.40) we finally get

$$\mu_2 = -\frac{\beta_2}{2\alpha'(0)} = -9.3726 \tag{3.51}$$

Because of the large absolute value of μ_2 in (3.51), the amplitude extimation given in (3.45) doesn't have practical value because it requires $|\mu| = R_0 - R \leqslant 0.1$.

The period of the oscillations near the bifurcation value may be computed from (2.15) and it gives:

$$T=\frac{2\pi}{\omega_0}\simeq 2.05 \tag{3.52}$$

In Fig. 2 an asymptotically stable periodic solution is shown at the parameter value $R=7$, both in the phase space and as oscillations of $N_1=N_1(t)$, $N_2=N_2(t)$ versus time.

The computed period (3.52) is in a good agreement with the period of the computer simulation shown in Fig. 2. Moreover, computer simulations show that all over the R interval $(0, R_0)$ we have closed orbitally asymptotically stable orbits around the equilibrium N^* and with a period which is increasing as $|\mu|$ increases. For example at $|\mu|=4.77$ the asymptotically stable closed orbit has period $T(\mu)\simeq 3.3$.

(3.ii) we have two Hopf bifurcation values at $R_{01}=0.3032$ and $R_{02}=7.6782$. Following the same procedure as that shown for (3.i), and in accordance with Lemma 3.2, at the bifurcation values we obtain:

$$\beta_2|_{R_{01}}=-0.044, \qquad \mu_2|_{R_{01}}>0, \qquad T_{01}\simeq 7.64 \tag{3.53}$$

$$\beta_2|_{R_{02}}=-0.194, \qquad \mu_2|_{R_{02}}<0, \qquad T_{02}\simeq 1.89. \tag{3.54}$$

Theorem 3.1 implies that the locally asymptotically stable equilibrium N^* bifurcates again for decreasing R at R_{02} toward orbitally asymptotically stable closed orbits. This follows from (3.54) where, according to the second of (3.50), since $\beta_2|_{R_{20}}<0$, the stable bifurcation can only occur for decreasing R.

From (3.53) we can state that the Hopf bifurcation at $R=R_{01}$ occurs for increasing values of R toward stable closed orbits. Computer simulations show that within the whole range of $R\in(R_{01}, R_{02})$ closed orbits exist and remain orbitally asymptotically stable (see fig. 3).

Already at $R=7$ (i.e. $|\mu|=0.6732$) the closed orbits have a great amplitude (see Fig. 4a); for decreasing values of R they reach a maximum amplitude, then it begins to decrease, whereas their period continues to increase. For example, at $R=0.4$ computer simulations suggest that we continue to have stable oscillations with a period near $T_{01}\simeq 7.64$ (see Fig. 4b).

Figure 5 shows that at R_{01} the orbitally asymptotically stable closed orbit degenerates in an infinity of closed orbits surrounding the equilibrium (centre point), all with the same period T_{01} computed from (2.15) at the bifurcation value R_{01}. These results are in accordance with the fact that the same pair of complex and conjugate eigenvalues of the characteristic equation(2.9)-(2.10) undergoes the two bifurcations above described, changing twice the sign of their real parts as R decreases (negative-positive-negative). The remaining two roots, say λ_3, λ_4, maintain their negative real parts for all $R\in\mathbb{R}_+$. In fact, from Corollary 2.2, when $R>R_{02}$ $\psi>0$ and this means that all the four eigenvalues have negative real part.

When $R=R_{02}$ a pair of complex conjugate eigenvalues, say λ_1 and λ_2, cross the imaginary axis and their real part remain positive for $R_{01}<R<R_{02}$, whereas the other two eigenvalues continue to have negative real parts: this follows from

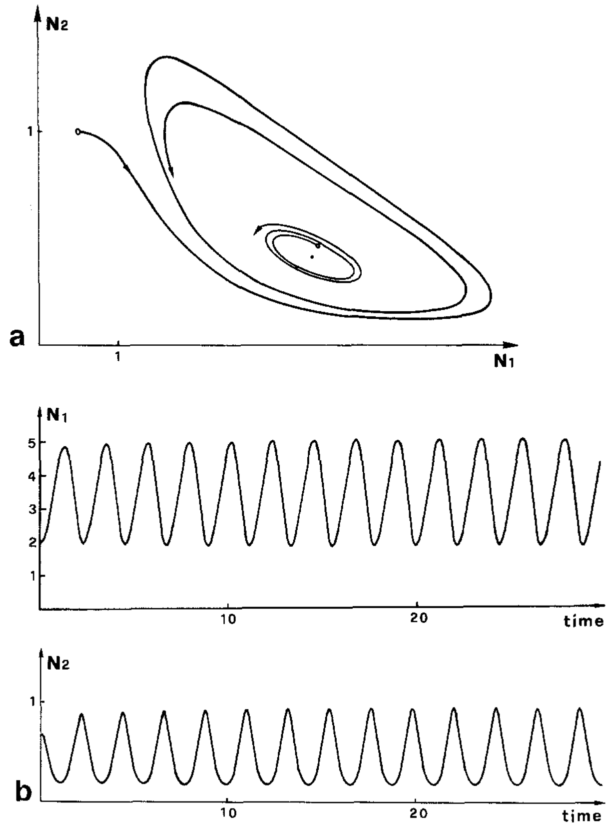

Fig. 2a, b. With the same set of values for parameters a_{12}, b_2, γ_2, e_2 as in Fig. 1, we fix the parameters $\alpha=2$, $\beta=3$ within region (i) of Fig. 1. The unique Hopf bifurcation occurs for decreasing R at $R_0=7.77$. Since $\beta_2=2\,\mathrm{Re}\,C_1(0)=-0.2254$ the bifurcation is toward orbitally asymptotically stable closed orbits. In the phase space $N_1\geq 0$, $N_2\geq 0$, for the value of parameter $R=7$, the periodic closed orbit asymptotically attracting two trajectories is shown by a computer simulation. One trajectory has initial conditions outside the limit cycle, and the other has initial conditions inside, near the equilibrium $N^*=(3.5, 0.4)$. **b** With the same parametric values, the oscillations of $N_1=N_1(t)$ and $N_2=N_2(t)$ are plotted versus time by a computer simulation. The computed period $T_0=2.05$ at the bifurcation value R_0 is in a good agreement with the period shown in **b**. In all the figures the initial conditions (2.1) are given assuming that in the past the system is at equilibrium, i.e. $N_i(t)=N_i^*$, $-\infty<t<0$, $i=1,2$, and then perturbing the equilibrium at $t=0$, i.e. $N_i(0)\neq N_i^*$, $i=1,2$

the fact that the function ψ has no zeros in that interval and from the positivity of the coefficient $a_1=a_1(R)$ (see (2.10)) for all $R\in\mathbb{R}_+$.

When $R=R_{01}$ a couple of eigenvalues cross the imaginary axis; but for $R<R_{01}$ all the eigenvalues must have negative real parts because $\psi>0$.

Thus λ_1 and λ_2 are the eigenvalues which change the sign of the real part, whereas λ_3 and λ_4 maintain the negative sign of their real part.

4. Discussion

We studied the qualitative behaviour of the model (1.1) as the nutrient supply R varies. The most remarkable result is that the presence of the nutrient-recycling

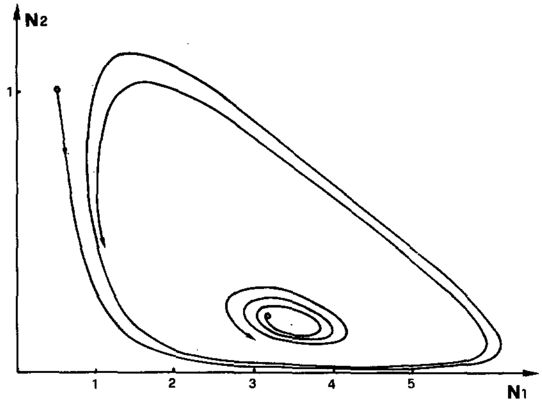

Fig. 3. With the same fixed set of values for parameters a_{12}, b_2, γ_2, e_2 as in Fig. 1, we fix the parameters $\alpha = 0.5$, $\beta = 4$ within the region (ii) of Fig. 1. The two Hopf bifurcation values are $R_{01} = 0.3032$, $R_{02} = 7.6782$. We fix $R = 3$. Although we are far from both the bifurcation values, the computer simulation shows the existence, in the positive orthant $\mathbb{R}^2_+ = \{(N_1, N_2) \in \mathbb{R}^2 N_i > 0, i = 1, 2\}$, of a closed orbit which is asymptotically attractive both from outside and from inside (excluding the positive equilibrium $N^* = (3.5, 0.171)$)

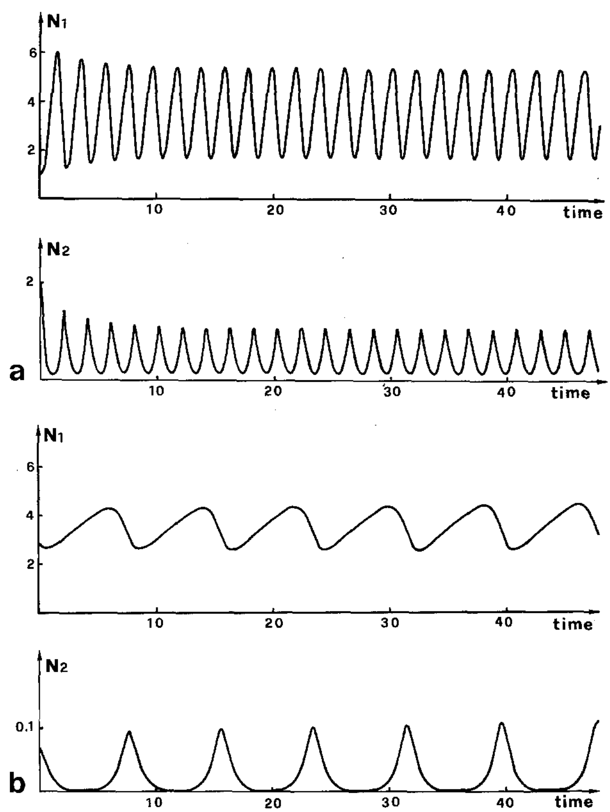

Fig. 4a, b. With the exception of parameter R, all other parametric values are the same as in Fig. 3. **a** shows the stable oscillations of $N_1 = N_1(t)$ and $N_2 = N_2(t)$ versus time when $R = 7 < R_{02} = 7.6782$. The computed period at the bifurcation value R_{02}, $T_{02} \simeq 1.89$, is in a good agreement with the period shown in **a**. **b** shows that the stable oscillations of N_1 and N_2 persist up to R values far from R_{02}, but near to R_{01}, i.e. $R = 0.4 > R_{01} = 0.3032$. Furthermore, decreasing R from R_{02} to R_{01} we have an impressive decreasing in the width of oscillations for the biotic species N_2 probably because of the decreasing of the equilibrium component N_2^* proportionally to R

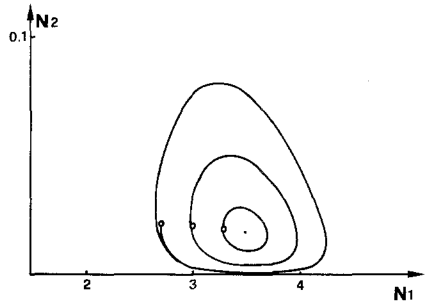

Fig. 5. We fix $R = R_{01} = 0.3032$. All other parametric values are the same as in Fig. 3. This figure shows that the asymptotically attractive closed orbit occurring within (R_{01}, R_{02}), at R_{01} degenerates to an infinity of closed orbits, all with the same period T_{01}, and one for each fixed initial condition

term with time lag in the first equation gives rise to the possibility of having two Hopf bifurcations when R varies. In fact it is easy to prove that if we set $b_2 = 0$ in model (1.1) (no recycling) we can have at most one Hopf bifurcation at $R = e_2(e_2 - \beta)/\gamma_2$ if $\beta < e_2$, i.e. if the average time lag $\bar{T}_\beta = 1/\beta$ is greater than the characteristic time of decay of the species $1/e_2$; in this case the positive equilibrium is locally asymptotically stable for $R > R_0$, whereas periodic orbits exist for $R < R_0$.

The presence of the recycling term with time lag allows the stability of the equilibrium at low values of R even if $\beta < e_2$; in fact in Sect. 2 we have shown that we can have two bifurcation values, $R_{01} < R_{02}$, such that the equilibrium is locally asymptotically stable for $R \in \mathbb{R}_+ - [R_{01}, R_{02}]$. The higher bifurcation value, R_{02}, is almost the same as the existing one without recycling, whereas the lower bifurcation value, R_{01}, is a consequence of the presence of the recycling term with time lag.

From Fig. 1 in Sect. 2 we can see that when α goes to infinity, i.e. the average time lag $\bar{T}_\alpha \to 0$, the model (1.1) can have at most one bifurcation value of R. Thus we can conclude that if $\beta < e_2$ model (1.1) has one bifurcation value either with $b_2 = 0$ or with $b_2 \neq 0$; the presence of the recycling term with time lag can introduce another Hopf bifurcation at a lower value of R provided that the time lag $\bar{T}_\alpha$ is great enough.

Furthermore the value of the parameter $b_2 \in (0, 1)$, which represents the extent of nutrient recycling, influences the period of oscillations. From (2.15) we have:

$$\omega_0^2 = \frac{a_3}{a_1} = \frac{\beta a_{12}(\alpha + e_2)\gamma_2 R_0}{e_2(\alpha + \beta)(a_{12} - b_2\gamma_2) + a_{12}\gamma_2 R_0}$$

and it is easy to see that if b_2 is increased, also ω_0^2 increases, therefore we conclude that the period $T_0 = 2\pi/\omega_0$ decreases as b_2 goes from 0 to 1.

By the Hopf bifurcation theory we proved, for a fixed set of parameters, the asymptotic stability of the bifurcating closed orbits near the bifurcation points. Computer simulations (see fig. 3) suggest that the orbits continue to exist and are stable on the whole interval $R \in (R_{01}, R_{02})$: as R varies from R_{01} to R_{02} we have a family of periodic orbits whose amplitude increases, reaches a maximum, then decreases again. By choosing α and β within the double bifurcation region we made a computer simulation in which the parameter R is increased in a discrete way (see fig. 6). The simulation shows that as R increases the biotic

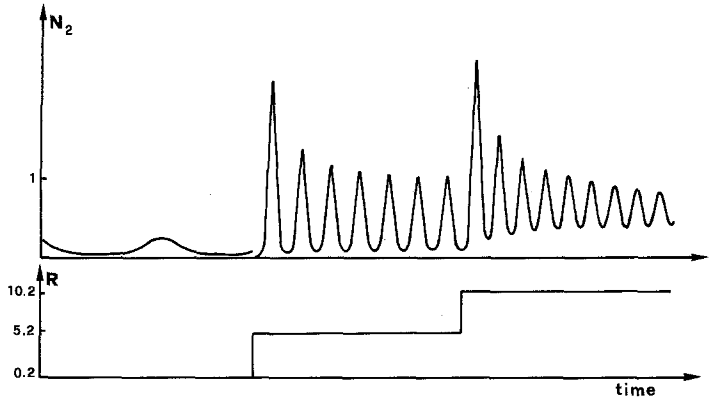

Fig. 6. Result of a computer simulation with a set of values of the parameters in the region of double bifurcation ($a_{12}=6$; $b_2=0.5$; $\gamma_2=2$; $e_2=7$; $\alpha=0.5$; $\beta=4$). N_2 is represented vs time and the parameter R changes during the simulation: we divide the time of simulation into 3 equal intervals.

During the first time interval we maintain $R=0.2<R_{01}$; then, for the following time-interval, we maintain R at the higher value $R=5.2$, i.e. $R_{01}<R<R_{02}$. Finally, in the third interval, we set R at the highest constant value $R=10.2>R_{02}$. In the first interval the scale of N_2 was expanded by a factor 10 because of the smallness of N_2^* for that value of R

species undergoes a transition from a low stable equilibrium to a higher stable equilibrium through stable oscillations. We note a sudden large increase of N_2 in correspondence with the two changes of the nutrient supply.

In model (1.1) R is assumed constant. Therefore the analysis of the dynamical behaviour of the model implicitly assumes that the system evolves on a time scale sufficiently fast to justify the assumption of a constant nutrient supply. This does not necessarily imply that the rate of nutrient supply R has always the same value. In a lake ecosystem it could be reasonable to assume that R may suddenly change on a seasonal time scale according to the step function shown in Fig. 6 and that in each period we have a different dynamical response of the model, as it is shown in Fig. 6 and according to the mathematical analysis presented in the paper.

Appendix 1

Computation of the coefficients $H_{20}(\theta)$ and $H_{11}(\theta)$ in (3.19). From its definition (3.17) the function $H(z,\bar{z},\theta)$ is given by

$$H(z,\bar{z},\theta):=F(w+2\,\mathrm{Re}\{zq(\theta)\})-2\,\mathrm{Re}\{g(z,\bar{z})q(\theta)\} \tag{A.1}$$

with

$$g(\bar{z},\bar{z})=q^*(0)'\cdot F(w+2\,\mathrm{Re}\{zq(0)\}).$$

Let us compute first the argument of F:

$$w+zq(\theta)+\bar{z}\bar{q}(\theta)=\begin{pmatrix} w^{(1)}(\theta)+z\,e^{i\omega_0\theta}+\bar{z}\,e^{-i\omega_0\theta} \\ w^{(2)}(\theta)+zB\,e^{i\omega_0\theta}+\bar{z}\bar{B}\,e^{-i\omega_0\theta}\end{pmatrix} \tag{A.2}$$

where (3.5) has been used. According with definition (3.3) of operator F

$$F(w+2\,\mathrm{Re}\{zq(\theta)\}):=\begin{cases}\begin{pmatrix}0\\0\end{pmatrix}, & -\infty<\theta<0\\ \begin{pmatrix}f_0^1\\f_0^2\end{pmatrix}, & \theta=0\end{cases} \tag{A.3}$$

where

$$\begin{aligned} f_0^1 &:= -a_{12}(w^{(1)}(0)+z+\bar{z})(w^{(2)}(0)+zB+\bar{z}\bar{B})\\ f_0^2 &:= \gamma_2(w^{(2)}(0)+zB+\bar{z}\bar{B})\left(\tilde{w}^{(1)}+\frac{\beta(\beta-i\omega_0)}{\beta^2+\omega_0^2}\,z+\frac{\beta(\beta+i\omega_0)}{\beta^2+\omega_0^2}\,\bar{z}\right)\end{aligned} \tag{A.3$'$}$$

with $\tilde{w}^{(1)}:=\int_{-\infty}^{0} w^{(1)}(s)\beta\, e^{\beta s}\, ds$. Let us observe that because of (3.14) and (A.3)$'$, w cannot contribute to H_{20}, H_{11} because it introduces only terms of higher order than z^2, $\bar{z}^2$, $z\bar{z}$. Furthermore, from (3.6) and (A.3)$'$

$$g(z,\bar{z})=\bar{D}f_0^1+\bar{D}\bar{C}f_0^2 \tag{A.4}$$

and finally:

$$H(z,\bar{z},\theta)=-2\,\mathrm{Re}(\bar{D}f_0^1(z,\bar{z})+\bar{D}\bar{C}f_0^2(z,\bar{z}))q(\theta)+\begin{cases}\begin{pmatrix}0\\0\end{pmatrix}, & -\infty<\theta<0\\ \begin{pmatrix}f_0^1(z,\bar{z})\\f_0^2(z,\bar{z})\end{pmatrix}, & \theta=0\end{cases} \tag{A.5}$$

Now, let us observe that

$$H_{20}=\left[\frac{\partial^2}{\partial z^2}H(z,\bar{z},\theta)\right]_{z=\bar{z}=0},\qquad H_{11}=\left[\frac{\partial^2}{\partial z\partial\bar{z}}H(z,\bar{z},\theta)\right]_{z=\bar{z}=0} \tag{A.6}$$

Let us first consider H_{20}. Then, by inspection of (A.3)$'$ we have:

$$\left[\frac{\partial^2}{\partial z^2}f_0^1(z,\bar{z})\right]_{z=\bar{z}=0}=-2a_{12}B,\qquad \left[\frac{\partial^2}{\partial z^2}f_0^2(z,\bar{z})\right]_{z=\bar{z}=0}=\frac{2\gamma_2B\beta(\beta-i\omega_0)}{\beta^2+\omega_0^2} \tag{A.7}$$

Therefore, if we define

$$\Gamma:=a_{12}B-\bar{C}\frac{\gamma_2\beta B(\beta-i\omega_0)}{\beta^2+\omega_0^2}, \tag{A.8}$$

then from (A.5), (A.7) we finally obtain (3.20). By the same procedure, we have that

$$\begin{aligned}\left[\frac{\partial^2 f_0^1(z,\bar{z})}{\partial z\partial\bar{z}}\right]_{z=\bar{z}=0}&=\left[\frac{\partial^2 \bar{f}_0^1(z,\bar{z})}{\partial z\partial\bar{z}}\right]_{z=\bar{z}=0}=-2a_{12}\,\mathrm{Re}\,B\\ \left[\frac{\partial^2 f_0^2(z,z)}{\partial z\partial\bar{z}}\right]_{z=\bar{z}=0}&=\left[\frac{\partial^2 \bar{f}_0^2(z,\bar{z})}{\partial z\partial\bar{z}}\right]_{z=\bar{z}=0}=\gamma_2B\beta\frac{\beta+i\omega_0}{\beta^2+\omega_0^2}+\gamma_2\bar{B}\beta\frac{\beta-i\omega_0}{\beta^2+\omega_0^2}\end{aligned} \tag{A.9}$$

From the definition (3.7) of B it is easy to recognize that:

$$\left[\frac{\partial^2}{\partial z \partial \bar{z}} f_0^2(z, \bar{z})\right]_{z=\bar{z}=0} = \left[\frac{\partial^2}{\partial z \partial \bar{z}} \bar{f}_0^2(z, \bar{z})\right]_{z=\bar{z}=0} = 0. \tag{A.10}$$

Hence, from (A.5), (A.9) and (A.10) we finally obtain (3.21).

Appendix 2

Solutions of (3.23) and (3.24).

Let us consider first the operator equation (3.23) where operator A is defined by (3.2) and $H_{20}(\theta)$ is given in (3.20). Explicitly writing (3.23) we obtain:

$$\begin{pmatrix} 2i\omega_0 - d/d\theta & 0 \\ 0 & 2i\omega_0 - d/d\theta \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(\theta) \\ w_{20}^{(2)}(\theta) \end{pmatrix} = \begin{pmatrix} 2\bar{D}\Gamma e^{i\omega_0\theta} + 2D\Gamma_1 e^{-i\omega_0\theta} \\ 2B\bar{D}\Gamma e^{i\omega_0\theta} + 2\bar{B}D\Gamma_1 e^{-i\omega_0\theta} \end{pmatrix}, \quad \theta \in (-\infty, 0), \tag{A.11}$$

whereas, when $\theta = 0$ we have:

$$\begin{pmatrix} 2i\omega_0 + a_{12}N_2^* & a_{12}N_1^* \\ 0 & 2i\omega_0 \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(0) \\ w_{20}^{(2)}(0) \end{pmatrix} - \int_{-\infty}^{0} \begin{pmatrix} 0 & b_2 e_2 \alpha e^{\alpha s} \\ N_2^* \gamma_2 \beta e^{\beta s} & 0 \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(s) \\ w_{20}^{(2)}(s) \end{pmatrix} ds = \begin{pmatrix} H_{20}^{(1)}(0) \\ H_{20}^{(2)}(0) \end{pmatrix}. \tag{A.12}$$

Before solving together (A.11) and (A.12) let us observe that, from the second of (3.12), $x_t(\theta) = w(\theta) + z(t)q(\theta) + \bar{z}(t)\bar{q}(\theta)$ for all $-\infty < \theta \leq 0$ and $t \in [0, +\infty)$.

By their definition $q(\theta)$ and $\bar{q}(\theta)$ are continuous functions of $\theta \in (-\infty, 0]$ and we must then require that also $w(\theta)$ be a continuous function of $\theta \in (-\infty, 0]$ to avoid a jump discontinuity for the solution $x_t(\theta) = x(t+\theta)$ at the actual time t obtained by putting $\theta = 0$.

Accordingly, we supplement the nonhomogeneous linear differential equations (A.11) by the boundary condition

$$\lim_{\theta \to 0^-} w_{20}(\theta) = w_{20}(0). \tag{A.13}$$

The same kind of boundary condition we require for the operator equation (3.24).

The general solution of (A.11) is given by:

$$\begin{aligned} w_{20}^{(1)}(\theta) &= \sigma_1 e^{i\omega_0\theta} \sigma_2 e^{-i\omega_0\theta} + \sigma_f e^{2i\omega_0\theta} \\ w_{20}^{(2)}(\theta) &= \mu_1 e^{i\omega_0\theta} + \mu_2 e^{-i\omega_0\theta} + \mu_f e^{2i\omega\theta} \end{aligned} \tag{A.14}$$

where $\sigma_f e^{2i\omega_0\theta}$, $\mu_f e^{2i\omega_0\theta}$ are solutions of the homogeneous part of (A.11). By direct substitution into (A.11) of the particular solutions of (A.14) we easily obtain σ_i, μ_i, $i = 1, 2$ given in (3.25c). (3.25d) trivially follows from the boundary condition (A.13) as applied to (A.14).

Now, by substitution of (A.14) into the integral part of (A.12) the following system of algebraic equations is obtained:

$$\begin{pmatrix} 2i\omega_0 + a_{12}N_2^* & a_{12}N_1^* - b_2 e_2 \alpha[(\alpha - 2i\omega_0)/(\alpha^2 + 4\omega_0^2)] \\ -N_2^* \gamma_2 \beta[(\beta - 2i\omega_0)/(\beta^2 + 4\omega_0^2)] & 2i\omega_0 \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(0) \\ w_{20}^{(2)}(0) \end{pmatrix} = \begin{pmatrix} C_{20}^{(1)} \\ C_{20}^{(2)} \end{pmatrix} \tag{A.15}$$

with

$$C_{20}^{(1)} = H_{20}^{(1)}(0) - \frac{i2b_2e_2\alpha}{\omega_0}\left[\frac{B\bar{D}\Gamma(\alpha - i\omega_0)}{\alpha^2+\omega_0^2} + \frac{\bar{B}D\Gamma_1(\alpha+i\omega_0)}{3(\alpha^2+\omega_0^2)} - \left(B\bar{D}\Gamma + \frac{\bar{B}D\Gamma_1}{3}\right)\frac{\alpha - 2i\omega_0}{\alpha^2+4\omega_0^2}\right]$$

$$C_{20}^{(2)} = H_{20}^{(2)}(0) + \frac{2N_2^*\gamma^2\beta}{i\omega_0}\left[\frac{\bar{D}\Gamma(\beta - i\omega_0)}{\beta^2+\omega_0^2} + \frac{D\Gamma_1(\beta+i\omega_0)}{3(\beta^2+\omega_0^2)} - \left(\bar{D}\Gamma + \frac{D\Gamma_1}{3}\right)\frac{\beta - 2i\omega_0}{\beta^2+4\omega_0^2}\right]. \tag{A.16}$$

Denoted by

$$\Delta = 2i\omega_0(2i\omega_0 + a_{12}N_2^*) + N_2^*\gamma_2\beta\frac{\beta - 2i\omega_0}{\beta^2+4\omega_0^2}\left(a_{12}N_1^* - b_2e_2\alpha\frac{\alpha-2i\omega_0}{\alpha^2+4\omega_0^2}\right), \tag{A.17}$$

the solutions of (A.15) are:

$$w_{20}^{(1)}(0) = \frac{2i\omega_0 C_{20}^{(1)} - \left(a_{12}N_1^* - b_2e_2\alpha\frac{\alpha - 2i\omega_0}{\alpha^2+4\omega_0^2}\right)C_{20}^{(2)}}{\Delta}$$

$$w_{20}^{(2)}(0) = \frac{(2i\omega_0 + a_{12}N_2^*)C_{20}^{(2)} + N_2^*\gamma_2\beta\frac{\beta-2i\omega_0}{\beta^2+4\omega_0^2}C_{20}^{(1)}}{\Delta} \tag{A.18}$$

Let us consider now the operator equation (3.24). We obtain:

$$\begin{pmatrix} -d/d\theta & 0 \\ 0 & -d/d\theta \end{pmatrix}\begin{pmatrix} w_{11}^{(1)}(\theta) \\ w_{11}^{(2)}(\theta)\end{pmatrix} = \begin{pmatrix} S\bar{D}\,e^{i\omega_0\theta} + SD\,e^{-i\omega_0\theta} \\ S\bar{D}B\,e^{i\omega_0\theta} + SD\bar{B}\,e^{-i\omega_0\theta}\end{pmatrix}, \qquad \theta \in (-\infty, 0) \tag{A.19}$$

where, for the sake of simplicity, we have set $S = 2a_{12}\,Re\,B$; and

$$\begin{pmatrix} a_{12}N_2^* & a_{12}N_1^* \\ 0 & 0\end{pmatrix}\begin{pmatrix} w_{11}^{(1)}(0) \\ w_{11}^{(2)}(0)\end{pmatrix} - \int_{-\infty}^{0}\begin{pmatrix} 0 & b_2e_2\alpha\,e^{\alpha s} \\ N_2^*\gamma_2\beta\,e^{\beta s} & 0\end{pmatrix}\begin{pmatrix} w_{11}^{(1)}(s) \\ w_{11}^{(2)}(s)\end{pmatrix}ds = \begin{pmatrix} H_{11}^{(1)}(0) \\ H_{11}^{(2)}(0)\end{pmatrix}, \qquad \theta = 0 \tag{A.20}$$

We supplement (A.19) with the boundary condition $\lim_{\theta\to 0^-} w_{11}(\theta) = w_{11}(0)$. The general solution of (A.19) is

$$w_{11}^{(1)}(\theta) = \rho_1\,e^{i\omega_0\theta} + \rho_2\,e^{-i\omega_0\theta} + \rho_f$$

$$w_{11}^{(2)}(\theta) = \chi_1\,e^{i\omega_0\theta} + \chi_2\,e^{-i\omega_0\theta} + \chi_f \tag{A.21}$$

where ρ_f, χ_f is the constant solution of the homogeneous part of (A.19), and the remaining part of (A.21) is a particular solution which directly substituted in (A.19), for ρ_i, χ_i, $i = 1, 2$, gives (3.27c). Furthermore, from the boundary condition (3.27d) follows.

Now, by substitution of (A.21) into the integral part of (A.20), we obtain the linear algebraic system:

$$\begin{pmatrix} a_{12}N_2^* & a_{12}N_1^* - b_2e_2 \\ -\gamma_2 N_2^* & 0 \end{pmatrix} \begin{pmatrix} w_{11}^{(1)}(0) \\ w_{11}^{(2)}(0) \end{pmatrix} = \begin{pmatrix} C_{11}^{(1)} \\ C_{11}^{(2)} \end{pmatrix} \tag{A.22}$$

where

$$\begin{aligned} C_{11}^{(1)} &= H_{11}^{(1)}(0) + i\frac{Sb_2e_2\alpha}{\omega_0}\left(B\bar{D}\frac{\alpha - i\omega_0}{\alpha^2+\omega_0^2} - \bar{B}D\frac{\alpha+i\omega_0}{\alpha^2+\omega_0^2} - \frac{1}{\alpha}(B\bar{D} - \bar{B}D)\right) \\ C_{11}^{(2)} &= H_{11}^{(2)}(0) - 2\frac{SN_2^*\gamma_2\beta}{\omega_0}\left(\frac{\operatorname{Im}(\bar{D}(\beta - i\omega_0))}{\beta^2+\omega_0^2} + \frac{\operatorname{Im}(D)}{\beta}\right), \end{aligned} \tag{A.23}$$

whose solution is:

$$w_{11}^{(1)}(0) = -\frac{C_{11}^{(2)}}{\gamma_2 N_2^*}; \qquad w_{11}^{(2)}(0) = \frac{N_2^*(a_{12}C_{11}^{(2)} + \gamma_2 C_{11}^{(1)})}{\gamma_2 R_0} \tag{A.24}$$

Appendix 3

Computation of $\tilde{w}_{20}^{(1)}$, $\tilde{w}_{11}^{(1)}$

To compute g_{21} (see 3.36) we need of $\tilde{w}_{20}^{(1)}$, $\tilde{w}_{11}^{(1)}$ as defined in (3.31).

By substitution of (A.14) and (A.21) in definitions (3.31) we easily obtain:

$$\begin{aligned} \tilde{w}_{20}^{(1)} &= \int_{-\infty}^{0} \beta\, e^{\beta s}(\sigma_1\, e^{i\omega_0 s} + \sigma_2\, e^{-i\omega_0 s} + (w_{20}^{(1)}(0) - \sigma_1 - \sigma_2)\, e^{2i\omega_0 s})\, ds \\ &= \beta\left(\sigma_1\frac{\beta - i\omega_0}{\beta^2+\omega_0^2} + \sigma_2\frac{\beta+i\omega_0}{\beta^2+\omega_0^2} + w_{20}^{(1)}(0)\frac{\beta - 2i\omega_0}{\beta^2+4\omega_0^2} - (\sigma_1+\sigma_2)\frac{\beta-2i\omega_0}{\beta^2+4\omega_0^2}\right) \end{aligned} \tag{A.25}$$

$$\begin{aligned} \tilde{w}_{11}^{(1)} &= \int_{-\infty}^{0} \beta\, e^{\beta s}(\rho_1\, e^{i\omega_0 s} + \rho_2\, e^{-i\omega_0 s} + (w_{11}^{(1)}(0) - \rho_1 - \rho_2)) \\ &= \beta\left(\rho_1\frac{\beta - i\omega_0}{\beta^2+\omega_0^2} + \rho_2\frac{\beta+i\omega_0}{\beta^2+\omega_0^2}\right) + w_{11}^{(1)}(0) - (\rho_1+\rho_2). \end{aligned} \tag{A.26}$$

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