SOME MODELS IN POPULATION DYNAMICS: STABILITY, LIMIT CYCLES, AND CHAOS

ARUN TEJASVI CHAGANTY *, RAMYA KORLAKAI VINAYAK †, AND GAURAV RAINA ‡

Abstract.
Biological systems are ripe with phenomenon occurring across various time scales, yet, conventional system design principles steer us away from exactly these phenomena. With the goal of understanding how traditional wisdom applies in this setting, we analyse how two simple population models, operating across two time scales, behave. We show that they capture a range of phenomenon from fixed points, to limit cycles, to chaos, and analytically characterise the stability of the fixed points, and limit cycles using Hopf bifurcation theory.

Key words. population model, stability, chaos, hopf bifurcation, center manifold theorem

AMS subject classifications. 37N25, 92D25, 93D99

1. Introduction. Feedback systems can be abundantly found in nature, from cellular chemical reactions, to the behaviour of large populations. When phenomena occur in well separated time scales, it is possible to isolate one of them and study it independent of the other. However, it is often the case that phenomena cooperate over comparable time scales, leading to interesting system dynamics.

Self-sustained oscillations which have been considered highly undesirable in engineering systems play a central role in almost any biological system. The study of limit cycles and their stability thus become important, for example, to predict the onset of cardiac arrhythmia.

In this paper, we analyse the delayed logistic equation and a similar quadratic population model proposed by Perez, Malta and Coutinho [1], which includes a forcing term. We show that while both exhibit fixed points and limit cycles, the former does not exhibit chaos to the best of our knowledge, while the former readily exhibits the same.

The paper is organised as follows: We will briefly describe the models we are studying in Section 2 and present analytic solutions in the absence of delay in Section 3. We then provide a sufficient condition for the stability of the fixed points of system with delay in Section 4 and show that Hopf bifurcations occur at the boundary of this region. We proceed to show the stability of the limit cycles produced at these Hopf bifurcations in Section 5. An overview of the chaos exhibited by our system is presented in Section 6. Finally, we summarise our conclusions and present further directions we wish to look at in Section 7. Additionally, we present some general results for the stability of the fixed points for a linear delay-differential equation in Appendix A and the stability of the local Hopf bifurcations for a quadratic delay differential equation in Appendix B.

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2. Model. We analyse two population models with quadratic delay-differential equations (DDEs). They can be written in the following general form,

$$\begin{aligned}\dot{x} &= \xi_x x(t) + \xi_y x(t-\tau) \\ &\quad + \xi_{xx} x^2(t) + \xi_{xy} x(t)\, x(t-\tau) + \xi_{yy} x^2(t-\tau)\,.\end{aligned} \tag{2.1}$$

The first model is the delayed logistic equation,

$$\begin{aligned}\dot{x} &= ax(t)\,(1 - bx(t-\tau)) \\ &= ax(t) - abx(t)\, x(t-\tau)\,,\end{aligned} \tag{2.2}$$

where $a, b > 0$ and $x(t) > 0$. This model is an extension of the famous logistic equation, first proposed by Verhulst in 1836 and then extended to include delays by Hutchinson. τ captures the gestation time of the species.

The second model is by Perez, Malta and Couthino [1] and is given by,

$$\begin{aligned}\dot{x} &= (a - bx(t-\tau))\, x(t-\tau) - cx(t) \\ &= -cx(t) + ax(t-\tau) - bx^2(t-\tau)\,,\end{aligned} \tag{2.3}$$

where $a, b, c > 0$ and $x(t) > 0$. This equation was proposed in 1978 as a model for laboratory adult blowfly populations and takes into account the gestation period τ required for an egg to become an adult fly. $x(t)$ represents the adult blowfly population at a given time t. The term $a - bx(t-\tau)$ models the birth-rate per head and c the death rate per head.

3. Analysis when $\tau = 0$. Before we consider the behaviour of the two systems across timescales, let us study their behaviour in a simpler setting, when $\tau = 0$.

3.1. Delayed Logistic Equation. Without delay, Equation 2.2 simplifies to the following quadratic equation,

$$\dot{x} = ax(t) - abx^2(t)\,. \tag{3.1}$$

This equation is analytically tractable and has the following solution,

$$x(t) = \begin{cases} \frac{1}{b + Ke^{-at}} & \text{if } 0 < x(0) < \frac{1}{b} \\ \frac{1}{b - Ke^{-at}} & \text{if } x(0) > \frac{1}{b}, \end{cases} \tag{3.2}$$

where $K > 0$ is a constant. It is clear that $x^* = \frac{1}{b}$ is the stable fixed point for this equation and $x^* = 0$ is the unstable one (Figure 3.1(a)).

3.2. Perez Malta Couthino Equation. Similarly, Equation 2.3 simplifies to the following quadratic equation,

$$\dot{x} = (a - c)\, x(t) - bx^2(t)\,, \tag{3.3}$$

with the following solution,

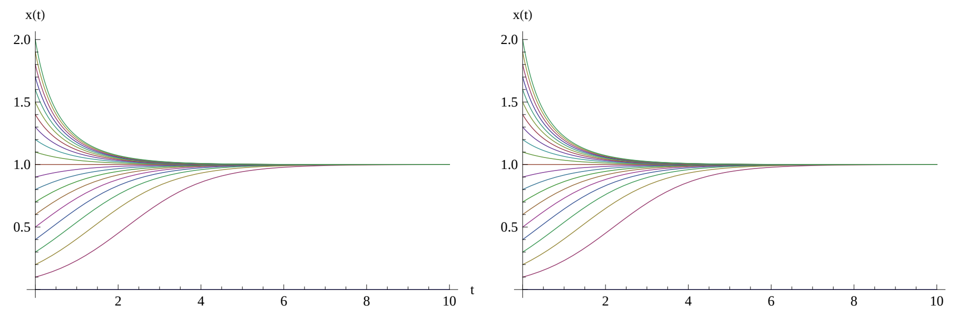
$$x(t) = \begin{cases} \frac{a-c}{b}\left(\frac{1}{1 - Ke^{-(a-c)t}}\right) & \text{if } x(0) > \frac{a-c}{b} \\ \frac{a-c}{b}\left(\frac{1}{1 + Ke^{-(a-c)t}}\right) & \text{if } x(0) < \frac{a-c}{b}, \end{cases} \tag{3.4}$$

with $K > 0$ is a constant. Of the two equillibria, $x^* = 0$ and $x^* = \frac{a-c}{b}$, it is clear that the former is stable when $a - c < 0$ and the latter when $a - c > 0$. Further more, when $a = c$, Equation 3.3 has the following solution,

$$x\left(t\right) = \frac{1}{bt + K}, \tag{3.5}$$

where K is a constant. In this case, $x^* = 0$ is a quasi-stable fixed point, i.e. it is stable when $x(t) > 0$ and unstable when $x(t) < 0$.

In the context of population dynamics, the system is of interest when $x^* > 0$, i.e. $a - c > 0$ (Figure 3.1(b)).



(a) Equation 2.2 with $a = 1.0$, $b = 1.0$ (b) Equation 2.3 with $a - c = 1.0$, $b = 1.0$

FIG. 3.1. *Equation 2.2 and Equation 2.3 with $\tau = 0$*

3.3. General Properties. When $a > c$, the equillibria of both Equation 2.2 and Equation 2.3 are equivalent; with a and b of Equation 2.2 being equivalent to $(a - c)$ and $\frac{b}{a-c}$ in Equation 2.3 respectively. It is not surprising then that the behaviour we see in Figure 3.1 is identical.

4. Stability of Fixed Points when $\tau > 0$. As we have seen in the previous section, the two equations have equivalent behaviour in the absence of delay. We will now the study the stability of the fixed points, x^* found in Section 3 in the presence of delay.

In general, a quadratic delay differential equation like Equation 2.1 can be linearised about x^* to,

$$\begin{aligned}\dot{x} &= (\xi_x + \xi_{xy}x^* + 2\xi_{xx})x(t)\\ &\quad + (\xi_y + \xi_{xy}x^* + 2\xi_{yy})x(t-\tau)\\ &\quad - (\xi_{xx} + \xi_{yy})x^*.\end{aligned}$$

Let $u(t) = x(t) - x^*$, then,

$$\begin{aligned}\dot{u} &= (\xi_x + \xi_{xy}x^* + 2\xi_{xx})u(t)\\ &\quad + (\xi_y + \xi_{xy}x^* + 2\xi_{yy})u(t-\tau).\end{aligned} \tag{4.1}$$

We state the following general theorem about the stability of the fixed points of a linear delay differential equation,

THEOREM 4.1. *(Necessary and Sufficient Conditions for Stability)*
A linear delay-differential equation of the form

$$\dot{x} = -ax\left(t\right) - bx\left(t - \tau\right),$$

has the following stability properties:

(i) The system is exponentially stable near 0 *for all* τ *when* $a > |b|$.

(ii) The system is stable near x^* *when* $0 < a \le b$, *and* $0 \le \tau < \tau_0$, *where,*

$$\tau_0 = \frac{\pi - \cos^{-1}(\frac{a}{|b|})}{\sqrt{b^2 - a^2}}. \tag{4.2}$$

(iii) The system undergoes Hopf bifurcations with respect to τ *when* $0 < a \le b$, *at* $\tau = \tau_0$. *Further,* $\mathbf{Re}\left(\frac{\partial}{\partial \tau}\lambda\right)\Big|_{\tau=\tau_k} > 0$.

Proof. See Appendix A. □

We can now apply this theorem to our two models.

COROLLARY 4.2. *(Stability of the Delayed Logistic Equation)* *Equation 2.2 exhibits the following stability properties:*

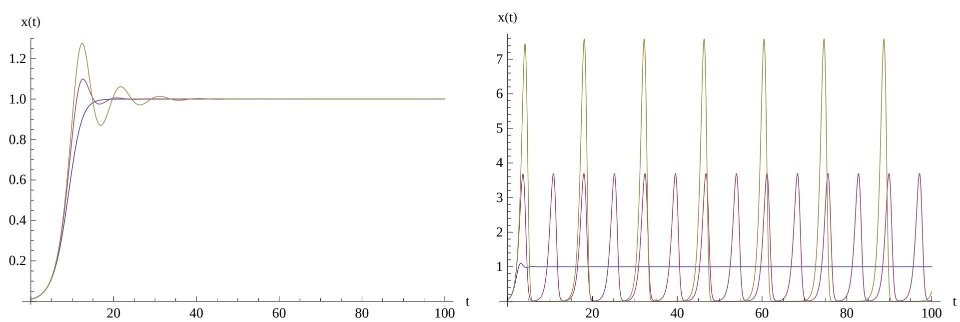
(i) $x^* = \frac{1}{b}$ *is exponentially stable for all* τ *when* $a < 1$ *and stable for* $\tau < \tau_0$ *when* $b \ge 1$, *where* τ_0 *is,*

$$\tau_0 = \frac{\pi}{2a}. \tag{4.3}$$

(ii) The system is undergoes Hopf bifurcations about $x^* = \frac{1}{b}$ *with respect to* τ *when* $a \ge 1$, *at* $\tau = \tau_0$. *Further,* $\mathbf{Re}\left(\frac{\partial}{\partial \tau}\lambda\right)\Big|_{\tau=\tau_0} > 0$.

Proof. The linearised delay differential equation for Equation 2.2 near $x^* = \frac{1}{b}$ is $\dot{u} = -au(t-\tau)$. Applying Theorem 4.1, we get (i) and (ii). □

We have plotted the behaviour of Equation 2.2 for $\tau \in [0, 3]$ in Figure 4.



(a) $a = 0.5$, $b = 1$ and $x(0) = 0.99$

(b) $a = 1.5$, $b = 1$ and $x(0) = 0.95$

FIG. 4.1. *Equation 2.2 for values of* $\tau \in [0, 3]$.

COROLLARY 4.3. *(Stability of the Perez-Malta-Couthino Equation)* *Equation 2.3 exhibits the following stability properties:*

(i) $x^* = 0$ *is an exponentially stable fixed point for all* τ *when* $a < c$ *and unstable otherwise* $(a \ge c)$.

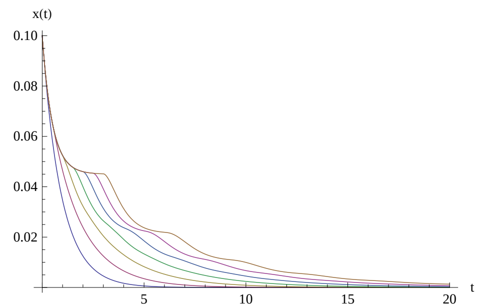
(ii) $x^* = \frac{a-c}{b}$ *is unstable for all* τ *when* $a < c$, *exponentially stable for all* τ *when* $c \le a < 3c$ *and stable for* $\tau < \tau_0$ *when* $a \ge 3c$. *where,*

$$\tau_0 = \frac{\pi - \cos^{-1}(\frac{c}{a-2c})}{\sqrt{(a-c)(a-3c)}}. \tag{4.4}$$

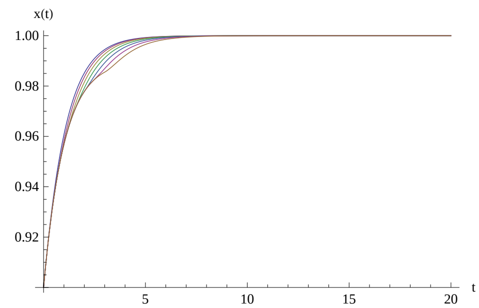
(iii) The system is undergoes Hopf bifurcations with respect to τ when $a \geq 3c$, at $\tau = \tau_0$. Further, $\mathbf{Re}\left(\frac{\partial}{\partial \tau}\lambda\right)\Big|_{\tau=\tau_0} > 0$.

Proof. The linearised delay differential equation for Equation 2.3 near $x^* = 0$ is $au(t-\tau) - cu(t)$. By Theorem 4.1, the system is exponentially stable when $c > a$ (Figure 4.2(a)), and unstable otherwise.

Near $x^* = \frac{a-c}{b}$, Equation 2.3 linearises to $\dot{u} = -cu(t) + (a-2c)u(t-\tau)$. Once again, using Theorem 4.1, the system is exponentially stable for all τ when $c > |a-2c|$, or when $c < a < 3c$ (Figure 4.2(b)).



(a) $a = 1$, $b = 1$, $c = 2$ and $x(0) = 0.01$



(b) $a = 2$, $b = 1$, $c = 1$ and $x(0) = 0.9$

FIG. 4.2. *Equation 2.3 for values of* $\tau \in [0, 3]$.

When $a \geq 3c$, the system is exponentially stable in the region $0 < \tau < \tau_0$, where,

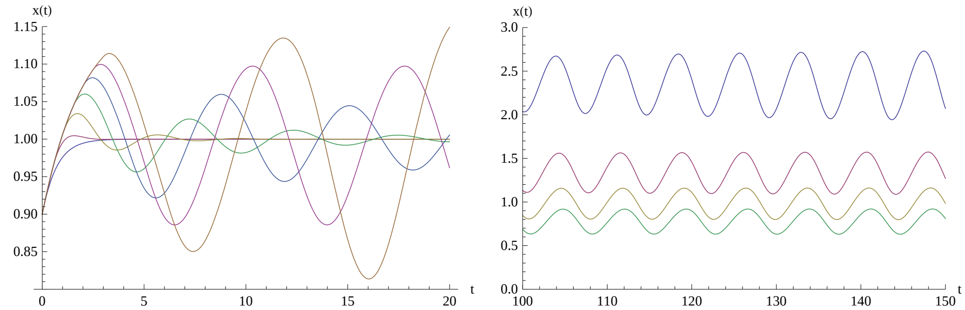
$$\begin{aligned}\tau_0 &= \frac{\pi - \cos^{-1}(\frac{c}{a-2c})}{\sqrt{(a-2c)^2 - c^2}} \\ &= \frac{\pi - \cos^{-1}(\frac{c}{a-2c})}{\sqrt{(a-c)(a-3c)}}.\end{aligned}$$

□

As noted in Theorem 4.1, $\tau = \tau_0$ is a Hopf bifurcation, and we expect the emergence of limit cycles, which is indeed the case (Figure 4.3(a), Figure 4.3(b)). The result that Hopf bifurcations occur in the Perez-Malta-Couthino equation only when $a > 3c$ tells us that oscillations about the stable fixed point occur only when the "positive feedback" term (a) is *significantly* larger than the "negative feedback" term (c), which is intuitive.

We note that the stability of the fixed points for both equations does not depend on b (the coefficent of the quadratic term). Thus, a forms a natural length scale for this model, and τ_0 a natural time scale. Using unit length scales for the two models, (i.e. $a = 1$ for Equation 2.2 and Equation 2.3) and using the results of Corollary 4.2 and Corollary 4.3, we have plotted the stability chart for both systems, in Figure 4.4. The behaviour at any a, will be a scaled version of the same.

We note that the stable region for Equation 2.2 is a strict subset of Equation 2.3. Comparing the two equations, the presence of the additional forcing term in Equation 2.3, $-cx(t)$ seems to be responsible for this increased region of stability. The bifurcation diagrams for the two systems in Figure 4.5 however, paints a different picture; the Perez-Malta-Couthino equation shows very evident chaotic behaviour,



(a) $a = 2$, $b = 1.5$, $c = 0.5$ and $x(0) = 0.9$

(b) $a = 1$, $c = 0.05$ and $x(0) = x^* - 0.1$

FIG. 4.3. *(a): Equation 2.3 for values of $\tau \in [0, 3]$, when $a > 3c$. Note the emergence of limit cycles. (b): Equation 2.3 for values of $b \in \{0.4, 0.7, 0.95, 1.2\}$ and $\tau = 1.89$. The stable limit cycle moves down when increasing b; the amplitude also decreases, but this can be ascribed to the decrease in relative magnitude of the initial displacement 0.1 to the parameters. Note that the value of τ used is greater than τ_0 in some cases, but still seems to have a stable limit cycle.*

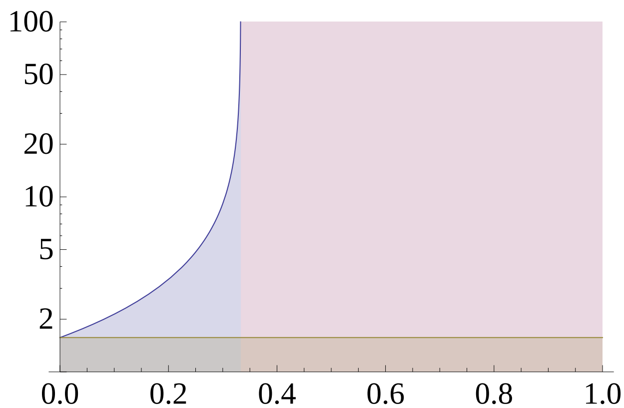


FIG. 4.4. *Stability Chart when $a = 1$. The shaded regions are stable. Green: Stable region for the delayed logistic equation. Blue: Stable region for the Perez Malta Couthino equation.*

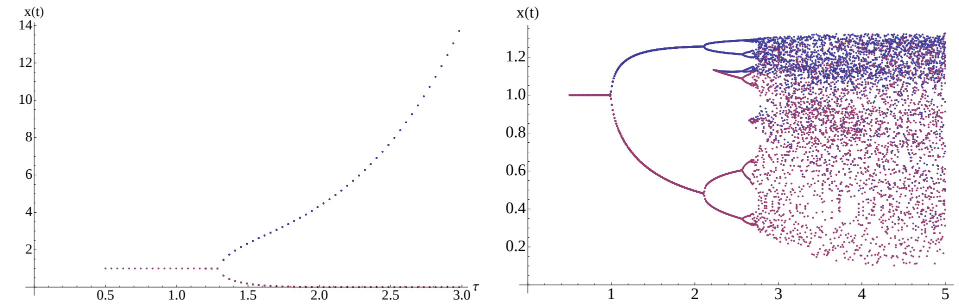
while the delayed logistic equation does not. We will look closer at this phenomenon in Section 6, after proving the stability of the Hopf bifurcations in Section 5.

5. Stability and Direction of Local Hopf Bifurcations. In the previous section, we saw empirical evidence from the bifurcation diagrams (Figure 4.5) the delayed logistic equation, Equation 2.2 and the Perez Malta Couthino equation, Equation 2.3, have stable limit cycles. In this section, we will analytically prove their stability using Hopf bifurcation theory.

THEOREM 5.1. *(Local Stability of Limit Cycles) A quadratic delay differential equation of the form,*

$$\begin{aligned}\dot{u} &= \xi_x u(t) + \xi_y u(t-\tau) \\ &\quad + \xi_{xx} u^2(t) + \xi_{xy} u(t) u(t-\tau) + \xi_{yy} u^2(t-\tau),\end{aligned}$$

can be reduced to the normal form of the Hopf bifurcation about $u^* = 0$. Let ω_0 be the (positive) eigenvalue of the linearised system at the Hopf bifurcation; this is the same



(a) Delayed Logistic Equation (b) Perez-Malta-Couthino

FIG. 4.5. *Bifurcation diagram for (a): Equation 2.2 when $a = 1$, $b = 1$ and (b): Equation 2.3 when $a = 1$, $b = 0.75$, $c = 0.25$*

as defined in Theorem 4.1. Let us define the following terms,

$$
\begin{aligned}
D &= \frac{1}{1 + \tau \xi_y e^{i\omega_0 \tau}} \\
G_{20} &= 2D \left(\xi_{xx} + \xi_{xy} e^{-i\omega_0 \tau} + \xi_{yy} e^{-2i\omega_0 \tau} \right) \\
G_{11} &= 2D \left(\xi_{xx} + \xi_{xy} \left(e^{-i\omega_0 \tau} + e^{i\omega_0 \tau} \right) \right) \\
&\quad + 2D \left(\xi_{yy} \right) \\
G_{02} &= 2D \left(\xi_{xx} + \xi_{xy} e^{i\omega_0 \tau} + \xi_{yy} e^{2i\omega_0 \tau} \right) \\
G_{21} &= 0 \\
G_{10} &= 2D \left(\xi_{xx} + \xi_{xy} \left(1 + e^{-i\omega_0 \tau} \right) \right) \\
&\quad + 2D \left(\xi_{yy} e^{-i\omega_0 \tau} \right) \\
G_{01} &= 2D \left(\xi_{xx} + \xi_{xy} \left(1 + e^{i\omega_0 \tau} \right) \right) \\
&\quad + 2D \left(\xi_{yy} e^{i\omega_0 \tau} \right). \\
c_1(0) &= \frac{i}{2\omega_0} \left(G_{20} G_{11} - 2|G_{11}|^2 - \frac{1}{3} |G_{02}|^2 \right) + \frac{G_{21}}{2} \\
\mu_2 &= -\frac{\mathbf{Re}\ c_1(0)}{\dot{\alpha}(0)} \\
\beta_2 &= 2\mathbf{Re}\ c_1(0).
\end{aligned}
$$

where $\alpha = \mathbf{Re}\ \lambda$, the real part of the Lyapunov exponent.

(i) The Hopf bifurcations of at $\tau = \tau_0$ are supercritical if $\mu_2 > 0$ and subcritical when $\mu_2 < 0$.

(ii) The system is asymptotically orbitally stable if $\beta_2 < 0$ and unstable otherwise.

Proof. See Appendix B. □

Noting that $\dot{\alpha}(0) = \mathbf{Re}\ (\frac{\partial}{\partial \tau}\lambda) \Big|_{\tau=\tau_0} > 0$ by Theorem 4.1, the sign of $\mu_2(0)$ is equivalent to the sign of $-\mathbf{Im}\ (G_{20}G_{11})$

To study the Hopf bifurcations about any general x^*, we can apply Theorem 5.1 to $u(t) = x(t) - x^*$;

$$
\dot{u} = \left(\xi_x + x^* \xi_{xy} + 2x^* \xi_{xx} \right) u(t) + \left(\xi_y + x^* \xi_{xy} + 2x^* \xi_{yy} \right) u(t - \tau)
$$

$$+\xi_{xx}u^2(t)+\xi_{xy}u(t)\,u(t-\tau)+\xi_{yy}u^2(t-\tau).$$

We now apply the theorem to our two equations.

To begin, let us write Equation 2.2 in the canonical form of Theorem 5.1 (noting $x^*=\frac{1}{b}$),

$$\begin{aligned}\dot{x}(t)&=ax(t)-abx(t)\,x(t-\tau)\\&=\left(a-ab\frac{1}{b}\right)u(t)+\left(-ab\frac{1}{b}\right)u(t-\tau)-abu(t)\,u(t-\tau)\\&=-au(t-\tau)-abu(t)\,u(t-\tau).\end{aligned}$$

Then,

$$\begin{aligned}\omega_0&=b\\D&=\frac{1}{1-a\tau e^{i\omega_0\tau}}\\G_{20}&=-2abDe^{-i\omega_0\tau}\\G_{11}&=-2abD\left(e^{-i\omega_0\tau}+e^{i\omega_0\tau}\right)\\G_{02}&=-2abDe^{i\omega_0\tau}\\G_{21}&=0\\G_{10}&=-2abD\left(1+e^{-i\omega_0\tau}\right)\\G_{01}&=-2abD\left(1+e^{i\omega_0\tau}\right)\\c_1(0)&=\frac{i}{2\omega_0}\left((2ab)^2D^2\left(1+e^{-i2\omega_0\tau}\right)-2(2ab)^2|D|^2-\frac{1}{3}(2ab)^2|D|^2\right).\end{aligned}$$

Consider the value of **Re** $c_1(0)$ at $\tau=\tau_0=\frac{\pi}{\omega_0}$,

$$\begin{aligned}\textbf{Re }c_1(0)&=\textbf{Re}\left(\frac{i}{2\omega_0}\left((2ab)^2D^2\left(1+e^{-i2\omega_0\tau}\right)-2(2ab)^2|D|^2-\frac{1}{3}(2ab)^2|D|^2\right)\right)\\&=\frac{(2ab)^2}{2\omega_0}\textbf{Im}\left(D^2\left(1+e^{-i2\omega_0\tau}\right)\right)\\&=\frac{(2ab)^2}{2\omega_0}\textbf{Im}\left(\frac{\left(1+e^{-i2\pi}\right)}{\left(1-a\frac{\pi}{b}e^{i\pi}\right)^2}\right)\\&=\frac{(2ab)^2}{2\omega_0}\textbf{Im}\left(\frac{2}{\left(1+a\frac{\pi}{b}\right)^2}\right)\\&=0.\end{aligned}$$

Therefore, both μ_2 and β_2 are 0 at the bifurcation point.

To begin, let us simplify Equation 2.3 to the canonical form of Appendix B. Let $u(t)=x(t)-x^*$, with , then,

$$\dot{x}(t)=ax(t-\tau)-bx^2(t-\tau)-cx(t)\tag{5.1}$$
$$\dot{u}(t)=(2c-a)\,u(t-\tau)-bu^2(t-\tau)-cu(t).\tag{5.2}$$

Then,

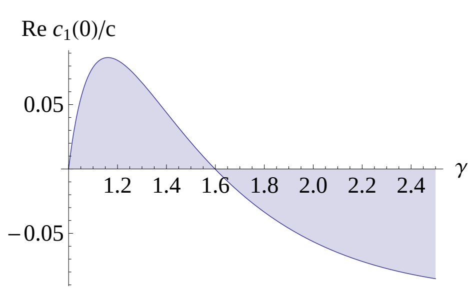
$$\omega_0=\sqrt{(2c-a)^2-c^2}$$

$$
\begin{aligned}
D &= \frac{1}{1-(a-2c)\,\tau e^{i\omega_0\tau}} \\
G_{20} &= -2bDe^{-i2\omega_0\tau} \\
G_{11} &= -2bD \\
G_{02} &= -2bDe^{i2\omega_0\tau} \\
G_{21} &= 0 \\
G_{10} &= -2bDe^{-i\omega_0\tau} \\
G_{01} &= -2bDe^{i\omega_0\tau} \\
c_1(0) &= \frac{i}{2\omega_0}\left((2b)^2 D^2 e^{-i2\omega_0\tau} - 2(2b)^2|D|^2 - \frac{1}{3}(2b)^2|D|^2\right).
\end{aligned}
$$

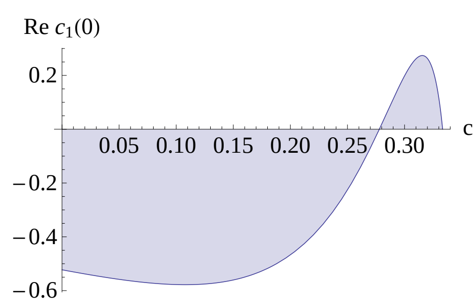
Let $a = 2c + \gamma c$, with $\gamma > 1$. Consider the value of $\mathbf{Re}\ c_1(0)$ at $\tau = \tau_0 = \frac{\pi - \cos^{-1}\frac{c}{a-2c}}{\omega_0} = \frac{\pi - \sec^{-1}\gamma}{\omega_0}$ and $\omega_0 = c\sqrt{\gamma^2-1}$,

$$
\begin{aligned}
\mathbf{Re}\ c_1(0) &= \mathbf{Re}\ \left(\frac{i}{2\omega_0}\left((2b)^2 D^2 e^{-i2\omega_0\tau} - 2(2b)^2|D|^2 - \frac{1}{3}(2b)^2|D|^2\right)\right) \\
&= \frac{(2b)^2}{2\omega_0}\mathbf{Im}\ \left(D^2 e^{-i2\omega_0\tau}\right) \\
&= \frac{2b^2}{c\sqrt{\gamma^2-1}}\mathbf{Im}\ \left(\frac{e^{-2i\left(\pi-\sec^{-1}(\gamma)\right)}}{\left(1-\frac{\gamma}{\sqrt{\gamma^2-1}}\left(\pi-\sec^{-1}(\gamma)\right)e^{i\left(\pi-\sec^{-1}(\gamma)\right)}\right)^2}\right).
\end{aligned}
$$

Plotting the value of $\frac{\mathbf{Re}\ c_1(0)}{c}$ versus $\gamma = \frac{a-2c}{c}$ (Figure 5.1(a)), we see that for all $\gamma > 1.6$, this value is negative and the bifurcations are supercritical. We have also plotted the magnitude of $\mathbf{Re}\ c_1(0)$ versus c in Figure 5.1(b).



(a) $\mathbf{Re}\ c_1(0)$ versus γ



(b) $\mathbf{Re}\ c_1(0)$ versus c

FIG. 5.1.

6. Chaotic Behaviour. The behaviour observed in Figure 4.5(b) and Figure 6.1 form strong evidence for chaos in the Perez-Malta-Couthino equation. By emperically analysing the values of τ at which new limit cycles are created, we observe that they seem to be spaced in a geometric sequence, roughly at $\tau_0, 2\tau_0, 2.5\tau_0, \cdots$. This is also characteristic of chaotic systems.

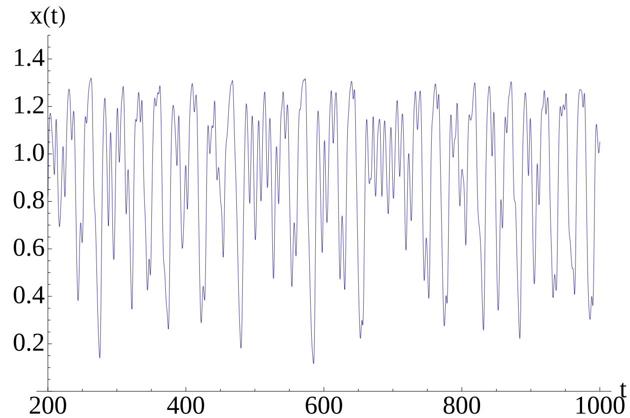


FIG. 6.1. *Equation 2.3 with $a = 2$, $b = 1.5$, $c = 0.5$, $\tau = 4.8\tau_0$, exhibiting chaotic behaviour.*

On the other hand, the bifurcation diagram for the delayed logistic equation (Figure 4.5(a)) is very regular and shows a stable limit cycle, though our analysis does not lend itself to this fact.

This behaviour is qualitatively different from the bifurcations in the linearised model,

$$\dot{x} = (a - 2bx^*)\, x\,(t - \tau) - cx\,(t)$$

in which the system has a limit cycle when $\tau = \tau_0$ and *diverges* for $\tau > \tau_0$. The presence of the quadratic negative feedback term prevents the system from "blowing up".

We would like to note that the logistic map,

$$x\,(t + 1) = rx\,(t)\,(1 - x\,(t))\,,$$

is embedded in the fixed points (i.e. when $\dot{x} = 0$) of the PMC equation,

$$\begin{aligned}
\dot{x} &= (a - bx\,(t - \tau))\, x\,(t - \tau) - cx\,(t)\\
cx\,(t) &= (a - bx\,(t - \tau))\, x\,(t - \tau)\\
x\,(t) &= \frac{b}{c}\left(\frac{a}{b} - x\,(t - \tau)\right) x\,(t - \tau)\,.
\end{aligned}$$

By considering $\frac{a}{b}$ to be the natural scale of $x(t)$ and $\frac{b}{c}$ as the canoncial paramter r, we see that the turning points of this system are exactly the solutions to the logistic map.

The logistic map is notable because it also gives rise to chaos, and the bifurcation diagram with respect to the parameter r is similar to our own, though our bifurcation parameter is τ. It would be interesting to explore if chaos can also be observed by varying $\tilde{r} = \frac{b}{c}$.

7. Concluding Remarks. We have analysed two population models with quadratic delay and shown that they behave similarly in the absence of delay. However, in the presence of a small delay, one system shows a larger region of stability due to the presence of a forcing term. Surprisingly though, the presence of this forcing term

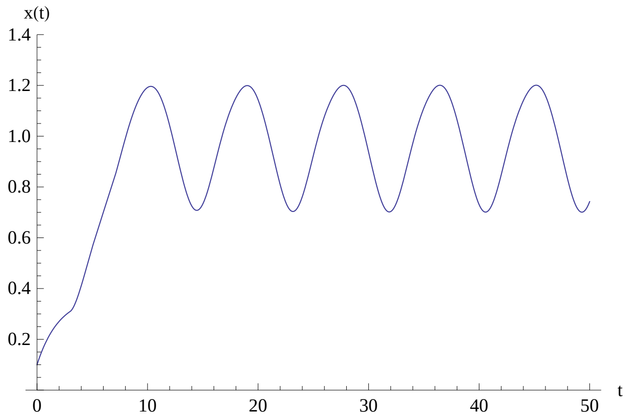


FIG. 7.1. *Equation 2.3 with $a = 2$, $b = 1.5$, $c = 0.5$, $\tau = 3$ and $x(0) = 0.1$. Note the convergence to the limit cycle.*

also introduces chaos to the system at larger values, which was absent in the latter equation.

As future work, we would like to analyse the global stability of our system; this is motivated by the behaviour in Figure 7.1, in which a trajectory starting far away from the fixed point, at $x(0) = 0.1$, also converges to a limit cycle about the fixed point at $x^* = 1$. We would also like to see if we can characterise analytically the chaotic phenomenon in the system.

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Appendix A. Linear Delay Differential Equations.

In this section, we will analyse the general linear delay differential equation (DDE),

$$\dot{x} = -ax\,(t) - bx\,(t-\tau)\,, \tag{A.1}$$

where $a > 0$, and $b \in \mathbb{R}$, and study it's stable regions.

We state the following theorem,

THEOREM A.1 (Sufficient Conditions for Stability). *Equation A.1 exhibits the following stability properties:*

(i) The system is exponentially stable for all τ when $a > |b|$.
(ii) The system is stable when $0 < a \leq b$, and $0 \leq \tau < \tau_0$, where,

$$\tau_0 = \frac{\pi - \cos^{-1}\left(\frac{a}{|b|}\right)}{\sqrt{b^2 - a^2}}.$$

(iii) The system undergoes Hopf bifurcations with respect to τ when $0 < a \leq b$, at $\tau = \tau_0$. Further, $\mathbf{Re}\,\left(\frac{\partial}{\partial \tau}\lambda\right)\Big|_{\tau=\tau_k} > 0$, where λ is the Lyapunov exponent.

Proof.
The characteristic equation of Equation A.1 is,

$$\lambda = -a - be^{-\lambda\tau}$$
$$\lambda + a + be^{-\lambda\tau} = 0. \tag{A.2}$$

Using $\lambda = \alpha + i\omega$,

$$\alpha + a + be^{-\alpha\tau}\cos(\omega\tau) + i\left(\omega - be^{-\alpha\tau}\sin(\omega\tau)\right) = 0$$

Equating real and imaginary parts to zero,

$$\alpha + a + be^{-\alpha\tau}\cos(\omega\tau) = 0$$
$$\cos(\omega\tau) = -\frac{\alpha + a}{b}e^{\alpha\tau} \tag{A.3}$$
$$\omega - be^{-\alpha\tau}\sin(\omega\tau) = 0$$
$$\sin(\omega\tau) = \frac{\omega}{b}e^{\alpha\tau}. \tag{A.4}$$

As a result of Equation A.3, we see that $\left|\frac{\alpha+a}{b}e^{\alpha\tau}\right| \leq 1$. For part (a) of the proof, we consider the case when $a > b$, and assuming that $\tau, \alpha > 0$, and arrive at a contradiction,

$$\left|\frac{(\alpha + b)}{a}e^{\alpha\tau}\right| > \left|\frac{\alpha}{b} + \frac{a}{b}\right| > 1.$$

Thus, when $a > b$, $\alpha < 0$ must necessarily hold, and consequentally, the system is exponentially stable. We note that when $a = b$, $\alpha = 0$ is a possibility. This completes part (i) of the theorem.

Let us now consider the case when $a \leq b$. In such a case, we note that when $\tau = 0$, the system is exponentially stable (as $a, b > 0$). Thus, let us find the *first* value for $\tau > 0$ such that the system is no longer stable, i.e. when $\mathbb{R}(\lambda) = \alpha = 0$. Equation A.3 and Equation A.4 would simplify to,

$$\cos(\omega\tau) = -\frac{a}{b}$$
$$\sin(\omega\tau) = \frac{\omega}{b}.$$

Solving for ω, we get,

$$\cos(\omega\tau)^2 + \sin(\omega\tau)^2 = \frac{a^2}{b^2} + \frac{\omega^2}{b^2}$$
$$a^2 + \omega^2 = b^2$$
$$\omega = \pm\sqrt{b^2 - a^2}.$$

Substituting this solution of ω into Equation A.3,

$$\cos(\omega\tau) = -\frac{a}{b}$$

$$\begin{aligned}
\tau_k &= \frac{2k\pi + \cos^{-1}\left(-\frac{a}{b}\right)}{\omega} \\
\tau_k &= \pm\frac{2k\pi + \cos^{-1}\left(-\frac{a}{b}\right)}{\sqrt{b^2 - a^2}} \\
\tau_k &= \pm\frac{(2k+1)\,\pi - \cos^{-1}\left(\frac{a}{b}\right)}{\sqrt{b^2 - a^2}}.
\end{aligned}$$

By considering the region between 0 and τ_0, we get part (ii) of the theorem. We remark that this is a Hopf bifurcation as the complex eigenvalues cross the imaginary axes ($\alpha = 0$) from left to right.

We require to show part (iii), to show that we satisfy the transversality condition of the Hopf spectrum, i.e.,

$$\mathbf{Re}\left(\frac{\partial}{\partial \tau}\lambda\right)\Big|_{\tau_k} \neq 0$$

To show this, differentiate Equation A.2,

$$\begin{aligned}
\frac{\partial}{\partial \tau}\lambda + be^{-\lambda\tau}\left(-\lambda - \tau\frac{\partial}{\partial \tau}\lambda\right) &= 0 \\
\frac{\partial}{\partial \tau}\lambda + (\lambda + a)\left(\lambda + \tau\frac{\partial}{\partial \tau}\lambda\right) &= 0 \\
\frac{\partial}{\partial \tau}\lambda\,(1 + \tau\,(\lambda + a)) + \lambda\,(\lambda + a) &= 0
\end{aligned}$$

At $\tau = \tau_k$, $\lambda = i\omega_0$,

$$\begin{aligned}
\mathbf{Re}\left(\frac{\partial}{\partial \tau}\lambda\right) &= \mathbf{Re}\left(\frac{\omega_0^2 - i\omega_0 a}{1 + a\tau + i\omega_0\tau}\right) \\
&= \frac{\omega_0^2}{(1 + a\tau)^2 + (\omega_0\tau)^2} \\
&> 0.
\end{aligned}$$

This completes the proof of Theorem 4.1. □

We have numerically plotted stability charts for the general linear DDE for different delays (A). We can see the stability region (when $b > 0$) shrinks as the delay increases, as expected.

Appendix B. Hopf Bifurcation Analysis.

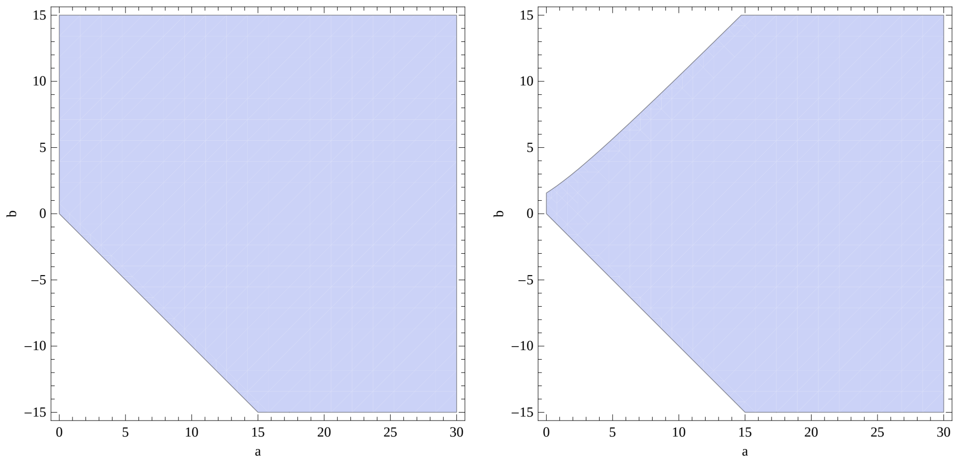
In this section, we will derive general results for the direction and stability of local Hopf bifurcations of a quadratic delay differential equation, along the lines of [2].

Consider a quadratic delay differential equation (DDE) with a stable equilibrium at $x^* = 0$,

$$\begin{aligned}
\dot{u}\,(t) &= \xi_x u\,(t) + \xi_y u\,(t - \tau) + \xi_{xx} u^2\,(t) \\
&\quad + \xi_{xy} u\,(t)\,u\,(t - \tau) + \xi_{yy} u^2\,(t - \tau)\,.
\end{aligned} \tag{B.1}$$

Our objective is to map Equation B.1 to a standard form for Hopf bifurcations,

$$\dot{z} = i\omega_0 z + g_{20}\frac{z^2}{2} + g_{11}\frac{z\bar{z}}{+} g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2}, \tag{B.2}$$



(a) $\tau = 0$ (b) $\tau = 1$

Fig. A.1. *Numerically plotted stability chart for the general linear DDE Equation A.1*

where $z, g_{ij} \in \mathbb{C}$ and $\omega_0 \in \mathbb{R}$.

Lemma B.1. *(Reduction to Standard Non-Linear Form) Equation B.1 can be written in the form,*

$$\dot{x} = A(\mu)\, x + F(x, \mu),$$

where $\mu \in \mathbb{R}$, $A(\alpha)$ is a smooth linear operator and $F(x, \alpha)$ is a smooth vector function containing non-linear terms.

Proof.

Let u_t be a bounded continuous function,

$$u_t(\theta) = u(t + \theta) \;\; u : [-\tau, 0] \to \mathbb{R},\;\; \theta \in [-\tau, 0].$$

We define the parametrised linear operator $\mathcal{L}_\mu$ acting on the space of bounded continuous functions $C[-\tau, 0]$ and $\mathcal{F} : C[-\tau, 0] \to \mathbb{R}$ be an operator that captures the non-linear terms. We assume that both $\mathcal{L}_\mu$ and $\mathcal{F}$ depend analytically on μ, the bifurcation parameter, atleast for small values of $|\mu|$. Let $\phi \in C[-\tau, 0]$, then the Riesz representation theorem guarantees us the existence of $\eta(\cdot, \mu) : [-\tau, 0] \to \mathbb{R}$ such that,

$$\begin{aligned} \mathcal{L}_\mu \phi &= \int_{-\tau}^{0} \mathrm{d}\eta(\theta, \mu)\, \phi(\theta) \\ &= \xi_x \phi(0) + \xi_y \phi(-\tau), \\ \mathrm{d}\eta(\theta, \mu) &= (\xi_x \delta(\theta) + \xi_x \delta(\theta + \tau))\, \mathrm{d}\theta. \end{aligned}$$

Further, we can define $\mathcal{F}(\phi, \mu)$ as follows,

$$\mathcal{F}(\phi, \mu) = \xi_{xx} \phi^2(0) + \xi_{xy} \phi(0)\, \phi(-\tau) + \xi_{yy} \phi^2(-\tau).$$

In particular, for $\phi = u_t$, we have,

$$\dot{u}(t) = \mathcal{L}_\mu u_t + \mathcal{F}(u_t, \mu) \tag{B.3}$$

where $t > 0, \mu \in \mathbb{R}$.

Finally, we can define,

$$\mathcal{A}(\mu)\phi(\theta) = \begin{cases} \frac{\partial}{\partial\theta}\phi(\theta), & \theta \in [-\tau, 0) \\ \mathcal{L}_\mu \phi, & \theta = 0 \end{cases}$$

$$\mathcal{R}\phi(\theta) = \begin{cases} 0, & \theta \in [-\tau, 0) \\ \mathcal{F}(\phi, \mu), & \theta = 0 \end{cases}$$

This allows us to write Equation B.3 as,

$$\dot{u}_t = \mathcal{A}(\mu) u_t + \mathcal{R} u_t. \tag{B.4}$$

This is of the required from, With $\mathcal{A}(\mu)$ and $\mathcal{R}$ being the linear and non-linear operators respectively. □

Lemma B.2. *By introducing a complex variable z, Equation B.4 can be written as a single equation,*

$$\dot{z} = \lambda(\mu) z + g(z, \bar{z}, \mu),$$

where $g = O(|z|^2)$ is a smooth function in $(z, \bar{z}, \mu)$. This system is topologically equivalent near the origin to,

$$\dot{z} = i\lambda z + g_{20}\frac{z^2}{2} + g_{11}\frac{z\bar{z}}{+} g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2}. \tag{B.5}$$

Proof. Let $q(\theta)$ be an eigenvector of $\mathcal{A}(\mu)$ (dependence on μ is dropped hereafter for notational convenience)

$$\begin{aligned} \mathcal{A}q(\theta) &= i\omega_0 q(\theta) \\ \mathcal{A}\bar{q}(\theta) &= -i\omega_0 \bar{q}(\theta) \\ q(\theta) &\propto e^{i\omega_0\theta}. \end{aligned}$$

The adjoint operator $\mathcal{A}^\dagger : C^1[0, \tau] \to \mathbb{R}$ will share the same eigenvalues,

$$\begin{aligned} \mathcal{A}^\dagger p(\zeta) &= -i\omega_0 p(\zeta) \\ \mathcal{A}^\dagger \bar{p}(\zeta) &= i\omega_0 \bar{p}(\zeta) \\ p(\zeta) &\propto e^{i\omega_0\zeta}. \end{aligned}$$

Using the inner product defined between $\psi \in C[0, \tau]$ and $\phi \in C[-\tau, 0]$,

$$\begin{aligned} \langle \psi, \phi \rangle = \psi^\dagger(0) \cdot \phi(0) \\ - \int_{\theta=-\tau}^{0} \int_{\zeta=0}^{\theta} \psi^\dagger(\zeta - \theta)\, \mathrm{d}\eta(\theta)\, \phi(\zeta)\, \mathrm{d}\zeta, \end{aligned}$$

we can normalise $p(\zeta) = De^{i\omega_0\zeta}$ with respect to $q(\theta) = e^{i\omega_0\theta}$,

$$\begin{aligned} \langle p, q \rangle &= \bar{D} - \int_{\theta=-\tau}^{0} \int_{\zeta=0}^{\theta} \bar{D} e^{i\omega_0(\theta-\zeta)+i\omega_0\zeta}\, \mathrm{d}\eta(\theta)\, \mathrm{d}\zeta \\ &= \bar{D} - \bar{D} \int_{\theta=-\tau}^{0} \theta e^{i\omega_0\theta} \left(\xi_x \delta(\theta) + \xi_y \delta(\theta + \tau)\right) \\ &= \bar{D} + \bar{D}\tau\xi_y e^{-i\omega_0\tau} \\ D &= \frac{1}{1 + \tau\xi_y e^{i\omega_0\tau}}. \end{aligned}$$

We now project our system onto the center manifold spanned by these eigenvectors,

$$
\begin{aligned}
z &= \langle p, u_t \rangle \\
\bar{z} &= \langle \bar{p}, u_t \rangle \\
w &= u_t - zq - \bar{z}\bar{q}.
\end{aligned}
\tag{B.6}
$$

Thus,

$$
\begin{aligned}
\dot{z} &= \langle p, \dot{u_t} \rangle \\
&= \langle p, \mathcal{A}u_t \rangle + \langle p, \mathcal{R}u_t \rangle \\
&= i\omega_0 z + \langle p, \mathcal{R}\left(zq + \bar{z}\bar{q} + w\right) \rangle \\
\dot{w} &= \dot{u_t} - \dot{z}q - \dot{\bar{z}}\bar{q} \\
&= \mathcal{A}w + \mathcal{R}u_t + \langle p, \mathcal{R}u_t \rangle q + \langle \bar{p}, \mathcal{R}u_t \rangle \bar{q} \\
&= \mathcal{A}w + \mathcal{R}\left(zq + \bar{z}\bar{q} + w\right) \\
&+ \langle p, \mathcal{R}\left(zq + \bar{z}\bar{q} + w\right) \rangle q \\
&+ \langle \bar{p}, \mathcal{R}\left(zq + \bar{z}\bar{q} + w\right) \rangle \bar{q}.
\end{aligned}
$$

Using Equation B.4, we note the following,

$$
\begin{aligned}
\langle p, \mathcal{R}u_t \rangle &= p\left(0\right) \cdot \mathcal{R}u_t\left(0\right) \\
&- \int_{\theta=-\tau}^{0} \int_{\zeta=0}^{\theta} p^{\dagger}\left(\zeta - \theta\right) \, \mathrm{d}\eta\left(\theta\right) \mathcal{R}\left(\zeta\right) \, \mathrm{d}\zeta \\
&= p\left(0\right) \cdot \mathcal{F}\left(u_t, 0\right) \\
&= p\left(0\right) \cdot \mathcal{F}\left(zq + \bar{z}\bar{q} + w, 0\right) \\
&= p\left(0\right) \cdot \mathcal{F}_0\left(z, \bar{z}, w\right) \\
\dot{z} &= i\omega_0 z + \langle p, \mathcal{F}_0\left(z, \bar{z}, w\right) \rangle \\
\dot{w} &= \mathcal{A}w + 2\mathbf{Re}\ \left(p\left(0\right) \cdot \mathcal{F}_0\left(z, \bar{z}, w\right) q\left(\theta\right)\right) \\
&+ \mathcal{F}_0\left(z, \bar{z}, w\right) \delta\left(\theta\right).
\end{aligned}
$$

Taking the Taylor Series' expansion to relevant order,

$$
\begin{aligned}
\dot{z} &= i\omega_0 z + \frac{1}{2}G_{20}z^2 + G_{11}z\bar{z} + \frac{1}{2}G_{02}\bar{z}^2 + \frac{1}{2}G_{21}z^2\bar{z} \\
&+ \langle G_{10}, w \rangle z + \langle G_{01}, w \rangle \bar{z} + \ldots \\
\dot{w} &= \mathcal{A}w + \frac{1}{2}H_{20}z^2 + H_{11}z\bar{z} + \frac{1}{2}H_{02}\bar{z}^2 + \ldots,
\end{aligned}
\tag{B.7}
$$

where G_{ij} are,

$$
\begin{aligned}
\mathcal{F}_0\left(z, \bar{z}, w\right) &= \xi_{xx}\left(zq\left(0\right) + \bar{z}\bar{q}\left(0\right) + w\right)^2 \\
&+ \xi_{xy}\left(zq\left(0\right) + \bar{z}\bar{q}\left(0\right) + w\right) \\
&\quad \left(zq\left(-\tau\right) + \bar{z}\bar{q}\left(-\tau\right) + w\right) \\
&+ \xi_{yy}\left(zq\left(-\tau\right) + \bar{z}\bar{q}\left(-\tau\right) + w\right)^2 \\
&= \xi_{xx}\left(z + \bar{z} + w\right)^2
\end{aligned}
$$

$$
\begin{aligned}
&+ \xi_{xy}\left(z+\bar{z}+w\right)\left(ze^{-i\omega_0\tau}+\bar{z}e^{i\omega_0\tau}+w\right)\\
&+ \xi_{yy}\left(ze^{-i\omega_0\tau}+\bar{z}e^{i\omega_0\tau}+w\right)^2\\
G_{20} &= p\left(0\right)\cdot\frac{\partial^2}{\partial z^2}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0}\\
&= p\left(0\right)\cdot 2\left(\xi_{xx}+\xi_{xy}e^{-i\omega_0\tau}+\xi_{yy}e^{-2i\omega_0\tau}\right)\\
G_{11} &= p\left(0\right)\cdot\frac{\partial^2}{\partial z\partial\bar{z}}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0}\\
&= p\left(0\right)\cdot 2\left(\xi_{xx}+\xi_{xy}\left(e^{-i\omega_0\tau}+e^{-i\omega_0\tau}\right)\right)\\
&+ p\left(0\right)\cdot 2\left(\xi_{yy}\right)\\
G_{02} &= p\left(0\right)\cdot\frac{\partial^2}{\partial\bar{z}^2}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0}\\
&= p\left(0\right)\cdot 2\left(\xi_{xx}+\xi_{xy}e^{i\omega_0\tau}+\xi_{yy}e^{2i\omega_0\tau}\right)\\
G_{21} &= p\left(0\right)\cdot\frac{\partial^3}{\partial z^2\partial\bar{z}}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0}\\
&= 0\\
G_{10} &= p\left(0\right)\cdot\frac{\partial^2}{\partial z\partial w}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0}\\
&= p\left(0\right)\cdot 2\left(\xi_{xx}+\xi_{xy}\left(1+e^{-i\omega_0\tau}\right)\right)\\
&+ p\left(0\right)\cdot 2\left(\xi_{yy}e^{-i\omega_0\tau}\right)\\
G_{01} &= p\left(0\right)\cdot\frac{\partial^2}{\partial\bar{z}\partial w}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0}\\
&= p\left(0\right)\cdot 2\left(\xi_{xx}+\xi_{xy}\left(1+e^{i\omega_0\tau}\right)\right)\\
&+ p\left(0\right)\cdot 2\left(\xi_{yy}e^{i\omega_0\tau}\right),
\end{aligned}
$$

and H_{ij} are,

$$
\begin{aligned}
H_{20} &= \frac{\partial^2}{\partial z^2}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0} - G_{20}q-\bar{G}_{02}\bar{q}\\
H_{11} &= \frac{\partial^2}{\partial z\partial\bar{z}}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0} - G_{11}q-\bar{G}_{11}\bar{q}\\
H_{02} &= \frac{\partial^2}{\partial\bar{z}^2}\mathcal{F}_0\left(z,\bar{z},w\right)\ \Big|_{z=0,w=0} - G_{02}q-\bar{G}_{20}\bar{q}.
\end{aligned}
$$

w can be represented in the center manifold as follows,

$$
w=\frac{1}{2}w_{20}z^2+w_{11}z\bar{z}+w_{02}\bar{z}^2+\dots,
$$

where w_{ij} are not known, but satisfy $\langle p, w_{ij}\rangle = 0$ as $w \in T^{su}$. We can find w_{ij} from Equation B.7,

$$
\begin{aligned}
\dot{w} &= \frac{1}{2}w_{20}\left(2z\dot{z}\right)+w_{11}\left(z\dot{\bar{z}}+\dot{z}\bar{z}\right)+w_{02}2\dot{\bar{z}}^2\\
i\omega_0 w_{20}z^2-i\omega_0 w_{02}\bar{z}^2 &= \mathcal{A}w+\frac{1}{2}H_{20}z^2+H_{11}z\bar{z}+\frac{1}{2}H_{02}\bar{z}^2.
\end{aligned}
$$

Thus we get,

$$\begin{aligned} w_{20} &= \left(2i\omega_0 I - \mathcal{A}\right)^{-1} H_{20} \\ w_{11} &= \left(-\mathcal{A}\right)^{-1} H_{11} \\ w_{02} &= \left(2i\omega_0 I + \mathcal{A}\right)^{-1} H_{02}. \end{aligned} \tag{B.8}$$

Substituting Equation B.8 in Equation B.7 and using Equation B.8, we finally get,

$$\begin{aligned} \dot{z} = {} & i\omega_0 z + \frac{1}{2} G_{20} z^2 + G_{11} z\bar{z} + \frac{1}{2} G_{02} \bar{z}^2 + \frac{1}{2} G_{21} z^2 \bar{z} \\ & - \langle G_{10}, \mathcal{A}^{-1} H_{11} \rangle z^2 \bar{z} \\ & + \frac{1}{2} \langle G_{20}, \left(2i\omega_0 I - \mathcal{A}\right)^{-1} H_{20} \rangle z^2 \bar{z}. \end{aligned} \tag{B.9}$$

Higher orders can safely be ignored, as per Lemma 3.2 in [3]. □

Having established that the delay differential equation Equation B.1 has a Hopf bifurcation, it's stability can be characterised using the following quantities,

$$\begin{aligned} c_1(0) &= \frac{i}{2\omega_0} \left(G_{20} G_{11} - 2|G_{11}|^2 - \frac{1}{3} |G_{02}|^2 \right) + \frac{G_{21}}{2} \\ \mu_2 &= -\frac{\mathbf{Re}\ c_1(0)}{\dot{\alpha}(0)} \\ \beta_2 &= 2\mathbf{Re}\ c_1(0). \end{aligned} \tag{B.10}$$

When $\mu_2 > 0$, the bifurcation is supercritical, and when $\mu_2 < 0$ the bifurcation is subcritical. The system is asymptotically orbtially stable if $\beta_2 < 0$ and unstable otherwise.