FFR110, Computational biology 1
Problem set 1

February 14, 2020

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Problem 1

Time delayed model with Allee effect

a) At T = 0.5 the obtained dynamics is no oscillations, see figure 1. At T = 3 the obtained dynamics is damped oscillations, which is visualised by the small oscillations at the start which are faded out in time, see figure 2. The plot with delay phase plane shows a stable spiral. At T = 4.5 the obtained dynamics is stable oscillations, which shows a limit cycle in the plot with delay phase plane, see figure 3.

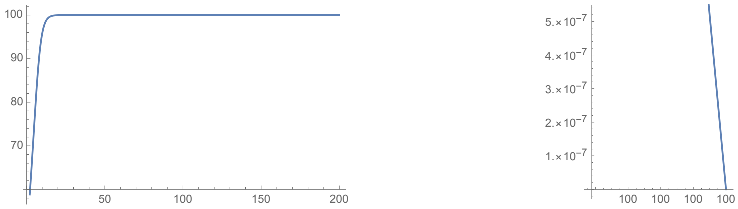

Figure 1: Dynamics showing no oscillations (T=0.5): a non oscillatory motion to the left ($tvs\dot{N}$) and neither a spiral nor a limit cycle to the right (delay phase plane).

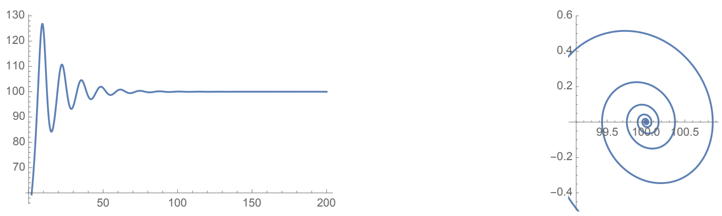

Figure 2: Dynamics showing damped oscillation (T=3): a damped oscillatory motion to the left ($t\ vs\ \dot{N}$) and a stable spiral to the right (delay phase plane).

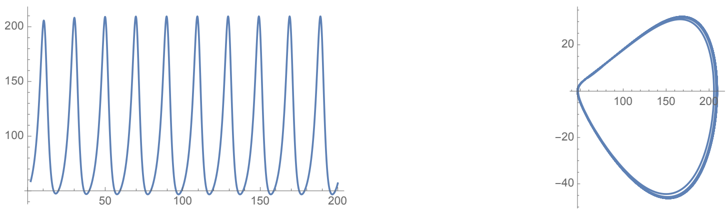

Figure 3: Dynamics showing stable oscillation (T=4.5): a stable oscillatory motion to the left ($t\ vs\ \dot{N}$) and a limit cycle to the right (delay phase plane).

b) At (approximately) T = 1.1 the dynamics starts exhibiting damped oscillations, i.e. small oscillations at the start which are faded out in time (first time when N>N*, can be visualized in a $t\ vs\ \dot{N}$ plot) as well as the start of a formation of a spiral (can visualized in a delay phase plane plot).

c) A Hopf Bifurcation occurs when a limit cycle or a periodic solution, that surrounds an equilibrium point, occurs or disappears as a parameter varies. In our case the parameter is the time delay T. In this case this occurs when the stable spiral changes into a limit cycle. This bifurcation occurs approximately at the point $T_H = 4.2$.

d) Analytically, we got that the bifurcation occurs at $T_H = 3.9270$ as follows:

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t-T)}{K}\right)\left(\frac{N(t)}{A} - 1\right)$$

set

$$\dot{N}(t) = N^* + \eta(t) \rightarrow$$

$$\frac{dN^*}{dt} + \dot{\eta}(t) = r\left(\eta(t) + N^*\right)\left(1 - \frac{N^* + \eta(t-T)}{K}\right)\left(\frac{N^* + \eta(t)}{A} - 1\right)$$

with

$$N^* = K \rightarrow$$

$$\dot{\eta}(t) = r\left(\eta(t) + K\right)\left(1 - \frac{K + \eta(t-T)}{K}\right)\left(\frac{K + \eta(t)}{A} - 1\right)$$

evaluate parenthesis and ignore all higher orders in terms of $\eta \rightarrow$

$$\dot{\eta}(t) = r * \frac{A - K}{A}\left(\eta(t-T)\right)$$

. With

$$\eta(t) = C * e^{\lambda t}$$

one gets

$$\lambda = \frac{A - K}{A} e^{-\lambda T} r$$

.

For a Hopfbifurcation $\lambda = i\omega$, which gives following expression

$$i\omega = \frac{A - K}{A} e^{-i\omega T} r$$

and further

$$i\omega = r\frac{A - K}{A}\left(\cos -\omega T + \sin -\omega T\right)$$

Since the equation is non-real on the left hand side, $\cos -\omega T = 0$, and thus $\omega T = \frac{\pi}{2}$. When $\omega T = \frac{\pi}{2}$, $sin{-}\omega T = \pm 1$ which finally gives $T_H = |\frac{\frac{\pi}{2}}{\pm\frac{K-A}{A}}| = 3.9270$. The analytically and numerically found bifurcation points differ with approximately 0.3. From this, one can assume that the numerical method is "accurate enough".

Problem 2

Discrete growth models

a) Steady states (fixed points) occurs when $F(N) = N_{\tau+1} = N_\tau$, and thus

$$N_{\tau+1} = \frac{(r+1)N_\tau}{1 + \left(\frac{N_\tau}{K}\right)^b} = N_\tau$$

The non-negative steady states of the model are $N_\tau^* = 0$ and $N_\tau^* = K \cdot \sqrt[b]{r}$, obtained from solving the above equation.

b) Linear stability analysis is performed as follows:

$$\frac{dN_{\tau+1}}{dN_\tau} = \frac{-(r+1)\left(b \cdot \left(\frac{N_\tau}{K}\right)^b - \left(\frac{N_\tau}{K}\right)^b - 1\right)}{\left(\left(\frac{N_\tau}{K}\right)^b + 1\right)^2}$$

Inserting the fixed points, one gets:

$$\frac{dN_{\tau+1}(0)}{dN_\tau} = r + 1$$

and

$$\frac{dN_{\tau+1}(K \cdot \sqrt[b]{r})}{dN_\tau} = 1 - \frac{b \cdot r}{r+1}$$

The fixed point $N_\tau^* = 0$ will always be unstable since $r > 0$. The stability of the other fixed point $N_\tau^* = K \cdot \sqrt[b]{r}$ depends on the parameters b and r. The point is stable when

$$\frac{b \cdot r}{r+1} < 2$$

and unstable when

$$\frac{b \cdot r}{r+1} > 2$$

c) As mentioned in previous section, $N_\tau^* = 0$ is always unstable and therefor no bifurcations occur around this fixed point with the parameter values given in this task. For the second fixed point, a bifurcation occur when

$$\frac{b \cdot r}{r+1} = 2$$

The stability of the fixed points are independent of K in both cases.

d) Figure 4 shows both the exact population dynamics and the approximation done by linearizing the population dynamics in the unstable fixed point, for each of the different initial population sizes. The liniarization of the dynamics in the unstable fixed point, done in b), gives the slope of the approximate curve to be $r+1$, with $r = 0.1$. The points for the approximation is gives by $N_{\tau+1} = \delta N_\tau \cdot 1.1$ where δN_τ is given by the distance to the unstable fixed point.

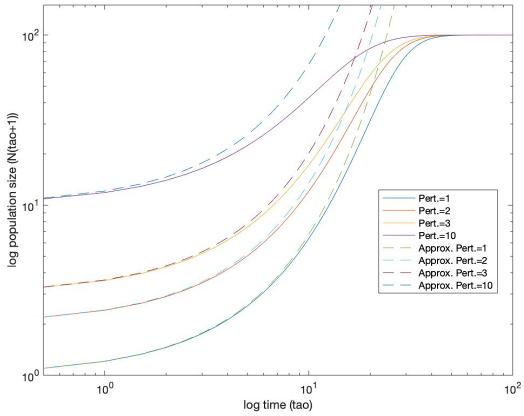

Figure 4: Population dynamics, both evaluated exact (solid line) and approximately with the linearized dynamics close to the unstable fixed point (dashed line).

e) From the figure, it is clear that the larger the perturbation is, the larger (and faster) does the approximation differ from the exact value. Instead of approaching the stable fixed point, as the exact dynamics does, the approximation goes to infinity. We believe that this is reasonable since one investigates how the dynamics acts close to the unstable fixed point when using the linearisation in the fixed point - how the dynamics acts close to the stable fixed point is not covered by this estimation. Close to the fixed point (for small τ), the approximation fits well to the exact solution - the smaller the initial value are (i.e. close to the fixed point) the better fit.

f) Figure 5 presents the exact dynamics and the approximation close to the stable steady state. The liniarization of the dynamics in the stable fixed point, done in b), gives the slope of the approximate curve to be $1 - \frac{b \cdot r}{r+1}$ with $r = 0.1$ $b = 1$. The points for the approximation is given by $N_{\tau+1} = N* + (1 - \frac{0.1}{1.1}) \cdot \delta N_\tau$ where N_τ is the distance to the stable fixed point.

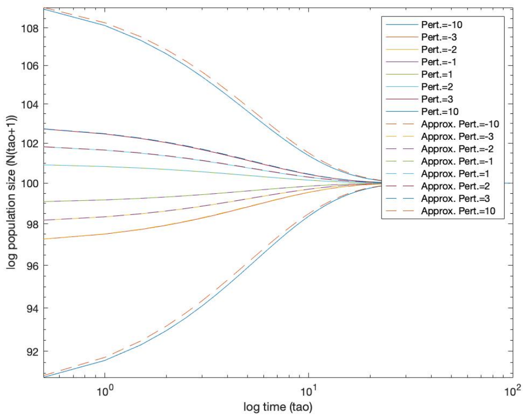

Figure 5: Population dynamics, both evaluated exact (solid line) and approximately with the linearized dynamics close to the unstable fixed point (dashed line).

As one can see from the figure, the closer the initial value are to the fixed point (smaller perturbation), the better does the approximation fit to the exact solution. One can also see that the approximation reaches the stable steady state from all initial values, which it did not do for the unstable steady state.

Problem 3

A route to chaos

a) A bifurcation diagram for

$$\eta_{\tau+1} = R\eta_\tau e^{-\alpha\eta_\tau}$$

was plotted as described in the task, and is presented in figure 6

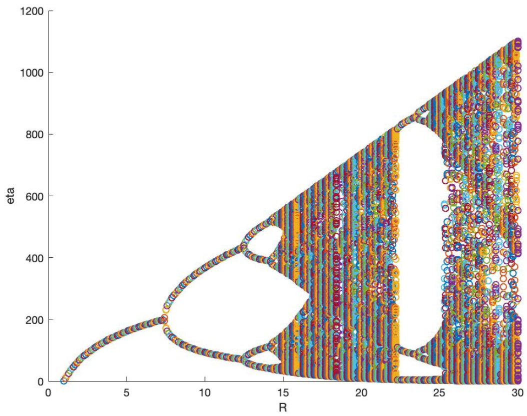

Figure 6: Bifurcation diagram for $\eta_{\tau+1} = R\eta_\tau e^{-\alpha\eta_\tau}$, with $\alpha = 0.01$, $\eta_\tau = 900$. R takes values between 1 and 30 in steps of 0.1. For each value of R the model ran for 300 generations. The last 100 generations for each R is plotted.

b) From figure 6 one can evaluate for what values of R, η_τ has a stable equilibrium, a 2-point cycle, a 3-point cycle and a 4-point cycle. Following values of R was chosen: $R_{Eq.} = 5$, $R_2 = 10$, $R_3 = 23$ and $R_4 = 14$. For each value of R the population dynamics where plotted, see figure 7 The dynamics for the stable equilibrium reaches a steady state

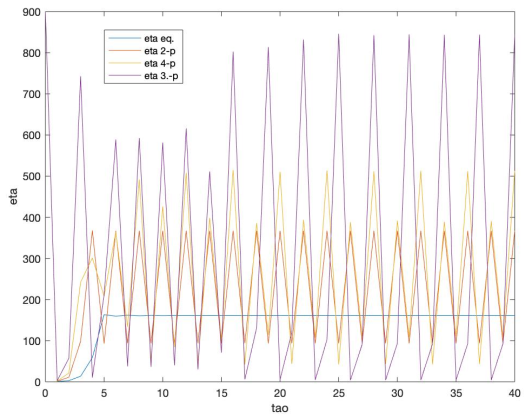

Figure 7: Plot of the population dynamics for 4 different representative values of R.

(equilibrium) fast, after a small oscillation. For the 2-point cycle, the dynamics reaches a stable oscillation almost instantly (faster than for the equilibrium case). The dynamics for the 4-point cycle reaches a stable oscillation with two periods (one with high amplitude and one with low), slightly slower than the two previous cases. For the 3-point cycle, the dynamics oscillates irregular before it reaches a stable oscillation.

c) From figure 6, one can see that the population dynamics bifurcate from a stable equilibrium to a stable 2-point cycle at $R_1 \approx 7.3$ and that the dynamics bifurcate to a stable 4-point cycle at $R_2 \approx 12.4$.

d) From the figure 8, it is possible to zoom in and see where the first R_∞ is, which is at approximately 15.1.

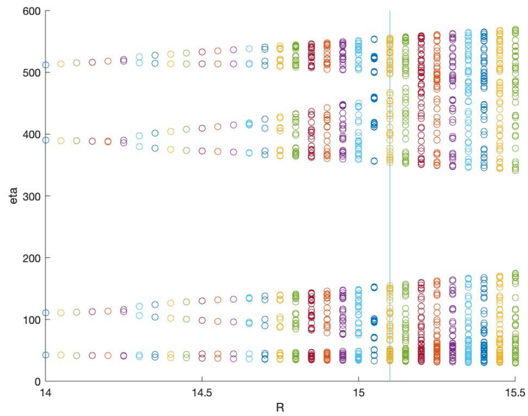

Figure 8: Zoomed in bifurcation diagram showing where R_∞ is approximated.

Matlab code

Exercise 1

```
%1a,b,c (written in mathematica)
k = 100;
A = 20;
r = 0.1;
Manipulate[Module[{x, t},
  Pane[Column[{Plot[
      Evaluate[
       x[t] /. First[
         NDSolve[{x'[t] == r*x[t]*(1 - x[t - T]/k)*(x[t]/A - 1),
           x[t /; t <= 0] == 50}, x, {t, 0, 200}]]], {t, 2, 200},
      PlotRange -> All, ImageSize -> {800, 400},
      AxesLabel -> {Style["t", FontSize -> 18],
        Style["N", FontSize -> 18]}],
     ParametricPlot[
      Evaluate[{x[t], x'[t]} /.
        First[NDSolve[{x'[t] == r*x[t]*(1 - x[t - T]/k)*(x[t]/A - 1),
           x[t /; t <= 0] == 50}, x, {t, 0, 200}]]], {t, 0, 200},
      AspectRatio -> 1.3, PlotRange -> All, ImageSize -> {800, 400},
      AxesLabel -> {Style["N", FontSize -> 18],
        Style["N'", FontSize -> 18]}]}],
   ImageSize -> {1600, 800}]],
 Delimiter, "time",
 {{T, 0.1, "T"}, 0.1, 5, .1, Appearance -> "Labeled"},
 TrackedSymbols :> {r, k, T}, ControlPlacement -> Left]
```

```
%% 1 D
A=20;
K=100;
r=0.1;
nVector=[0 1 2 3 4 5 6 7 8 9 10];
for i=1:11;
n=nVector(i);
T(i)=abs(A/(r*(K-A))*(1/2+n)*pi)
end
ans=T(1)
```

Exercise 2

```
%% 2 d)
clear
clc

K=10^3;
r=0.1;
b=1;
time=200;
Fp=0;
NVector=[1 2 3 10];

for j=1:4
    N(1,j)=NVector(j);
    for k=1:time
    N(k+1,j)=((r+1)*(N(k,j)))/(1+(N(k,j))/K);
    end
end

x=linspace(0,100,201);
y1=N(:,1);
y2=N(:,2);
y3=N(:,3);
y4=N(:,4);
```

```
loglog(x,y1,x,y2,x,y3,x,y4)
hold on
xlabel('log time (tao)')
ylabel('log population size (N(tao+1))')
N2(1,:)=[1 2 3 10];
deltaN(1,:)=[1 2 3 10];
slope=(r+1);

for j=1:4
    for k=1:time
        N2(k+1,j)=slope*deltaN(k,j);
        deltaN(k+1,j)=N2(k+1,j);
    end
end

x=linspace(0,100,201);
y12=N2(:,1);
y22=N2(:,2);
y32=N2(:,3);
y42=N2(:,4);

loglog(x,y12,'--',x,y22,'--',x,y32,'--',x,y42,'--')
legend('Pert.=1','Pert.=2','Pert.=3','Pert.=10','Approx. Pert.=1','Approx. Pert.=2','Approx.↩
    Pert.=3','Approx. Pert.=10')
ylim([10^0 1.5*10^2])
```

```
%% 2f
clear
clc

K=10^3;
r=0.1;
b=1;
time=200;

Fp=K*(r)^1/b;

NVector=[-10+Fp -3+Fp -2+Fp -1+Fp 1+Fp 2+Fp 3+Fp 10+Fp];

for j=1:8
    N(1,j)=NVector(j);
    for k=1:time
    N(k+1,j)=((r+1)*(N(k,j)))/(1+(N(k,j))/K);
    end
end

x=linspace(0,100,201);
y1=N(:,1);
y2=N(:,2);
y3=N(:,3);
y4=N(:,4);
y5=N(:,5);
y6=N(:,6);
y7=N(:,7);
y8=N(:,8);

loglog(x,y1,x,y2,x,y3,x,y4,x,y5,x,y6,x,y7,x,y8)
hold on
xlabel('log time (tao)')
ylabel('log population size (N(tao+1))')

Fp=K*(r)^1/b;

deltaN(1,:)=[-10 -3 -2 -1 1 2 3 10];
nStar=Fp;
slope=1-(b*r)/(r+1);

for i=1:8
    for j=1:time
    N2(j,i)=nStar+deltaN(j,i);
    deltaN(j+1,i)=slope*deltaN(j,i);
    end

end
```

```
x=linspace(0,100,200);
y12=N2(:,1);
y22=N2(:,2);
y32=N2(:,3);
y42=N2(:,4);
y52=N2(:,5);
y62=N2(:,6);
y72=N2(:,7);
y82=N2(:,8);

loglog(x,y12,'--',x,y22,'--',x,y32,'--',x,y42,'--',x,y52,'--',x,y62,'--',x,y72,'--',x,y82,'↩
    --')
legend('Pert.=-10','Pert.=-3','Pert.=-2', 'Pert.=-1','Pert.=1','Pert.=2','Pert.=3','Pert.=10↩
    ','Approx. Pert.=-10','Approx. Pert.=-3','Approx. Pert.=-2', 'Approx. Pert.=-1','Approx. ↩
    Pert.=1','Approx. Pert.=2','Approx. Pert.=3','Approx. Pert.=10')
xlabel('log time (tao)')
ylabel('log population size (N(tao+1))')
```

Exercise 3

```
%% 3a,d
clc
clf
clear

alpha=0.01;
eta(1)=900;

rVector=[5 10 14 23];
for j=1:length(rVector)
    R=rVector(j);
for i=1:40
    eta(i+1)=R*eta(i)*exp(-alpha*eta(i));
end
etaMatrix(j,:)=eta;
end

y=[etaMatrix(1,:); etaMatrix(2,:); etaMatrix(3,:);etaMatrix(4,:)];
x=0:40;
plot(x,y(1,:),x,y(2,:),x,y(3,:),x,y(4,:))
legend('eta eq.','eta 2-p','eta 4-p','eta 3.-p')
 xlabel('tao')
 ylabel('eta')
```

```
%% 3c
clc
clf
clear


alpha=0.01;
eta(1)=900;

rVector=[5 10 14 23];
for j=1:length(rVector)
    R=rVector(j);
for i=1:40
    eta(i+1)=R*eta(i)*exp(-alpha*eta(i));
end
etaMatrix(j,:)=eta;
end

y=[etaMatrix(1,:); etaMatrix(2,:); etaMatrix(3,:);etaMatrix(4,:)];
x=0:40;
plot(x,y(1,:),x,y(2,:),x,y(3,:),x,y(4,:))
legend('eta eq.','eta 2-p','eta 4-p','eta 3.-p')
 xlabel('tao')
 ylabel('eta')
```