Bio 417 Homework 1

Part 1 (for the week of Jan 28th, due Feb 11th)

1. (Gompertz equation) Another model of negative density dependence is the Gompertz equation, which is given by:

$$\frac{dN}{dt} = -aN \ln(bN) ,$$

where a and b are positive constants.
a) Plot the flow diagram of the system, identify the equilibria and their stability, both using the graphical method, and using linear stability analysis.

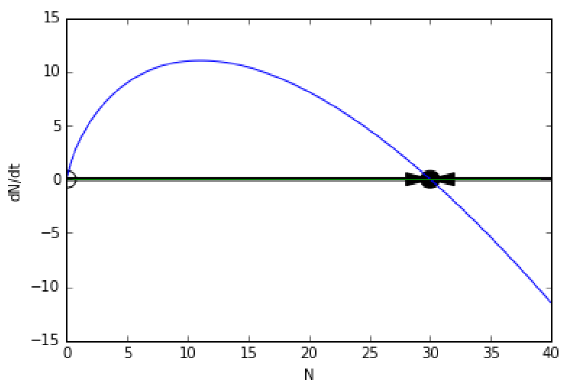

Figure 1: The flow diagram of the system (with $a = 1$ and $b = 1/30$). The stable equilibrium is marked with the filled circle, the unstable with the open.

For the linear stability analysis, the derivative of the right-hand-side of the dynamics is:

$$-a - a \ln(bN) , \tag{1}$$

which goes to $+\inf$ when $N \to 0$ and $-a$ when $N = 1/b$. Hence, the equilibrium at $N = 0$ is unstable while that at $N = 1/b$ is stable.

b) What is the biological interpretation of the coefficients a and b?

The parameter a gives the intrinsic growth rate of the population: how fast it increases or decreases, similar to r in the logistic equation. The parameter b on the other hand, determines when the population growth goes from positive to negative, and hence, the carrying capacity of the population. In particular, dN/dt becomes zero when $n = 1/b$, meaning that b is the inverse of the carrying capacity of the population.

c) This equation is found to be a good approximation for tumor growth in cancer, except for very small tumor sizes (small N). Explain, based on the equation, why the failure at small tumor sizes is not surprising.
Consider the per capita growth rate (i.e., the right-hand side divided by N): $-\ln(bN)$ The natural logarithm is unbounded (i.e., goes to negative infinity) as N goes to zero. But of course, real cells have a finite potential reproductive output: even at very small population sizes, no real cell can produce infinite numbers of offspring. Hence, at small N, the model becomes unrealistic.

2. (Intermittency) Consider the discrete logistic map:

$$x_{t+1} = \lambda x_t(1 - x_t)$$

a) Using the code in the iPython notebook, plot some trajectories for $\lambda = 3.828$. What do you observe?

The observation is that the system seems to show periodic-looking behavior for stretches but then intermittently plunges into chaos and comes back to periodicity. The intervals of periodicity and chaos seem not regular. This phenomenon is called intermittency. b) Plot the map resulting from applying the logistic map 3 times in succession. How does this map explain the behavior you observe in the trajectories? What happens when you increase λ slightly (say, by 0.001)?

See Figure 3, and its caption.

c) Discuss the potential biological consequences of the dynamical behavior you observed in part (a).

Intermittent dynamics means that you can have stable-looking population cycles that are interrupted with chaotic patterns that appear with unpredictable frequency. This kind of behavior usually happens when a stable cycle is just appearing (or disappearing, depending on the direction the parameters are moving), and therefore

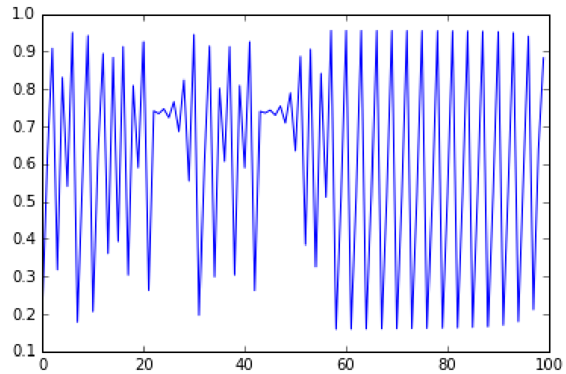

Figure 2: A sample trajectory showing intervals of cyclic behavior interspersed by irregular dynamics.

can be used as an "early signal" for how regime shifts can change population dynamics.

3. (Limits of the logistic map) The logistic map is customarily considered with λ between 0 and 4, and x between 0 and 1. Explain why these limits make sense. (Hint: show that for $x_0 > 1$, x will eventually go to $-\infty$.)

Since x is supposed to be a population size, negative x doesn't make sense, and any $x > 1$ will map to a negative number. Therefore $1 > x > 0$ makes sense. Now, if x is a negative number, it will map onto another negative number larger in magnitude when $\lambda \geq 1$ (since $1-x > 1$ for $x < 0$). Now, the maximum of $x(1-x)$ is at $x = 0.5$, which yields $x(1-x) = 0.25$. If $\lambda > 4$, this means $\lambda x(1-x) > 1$ for some region of x around 0.5, meaning that x will get mapped to above 1, and therefore the system will tend to negative infinity eventually. Hence these two limits ensure that the system stays bounded between 0 and 1.

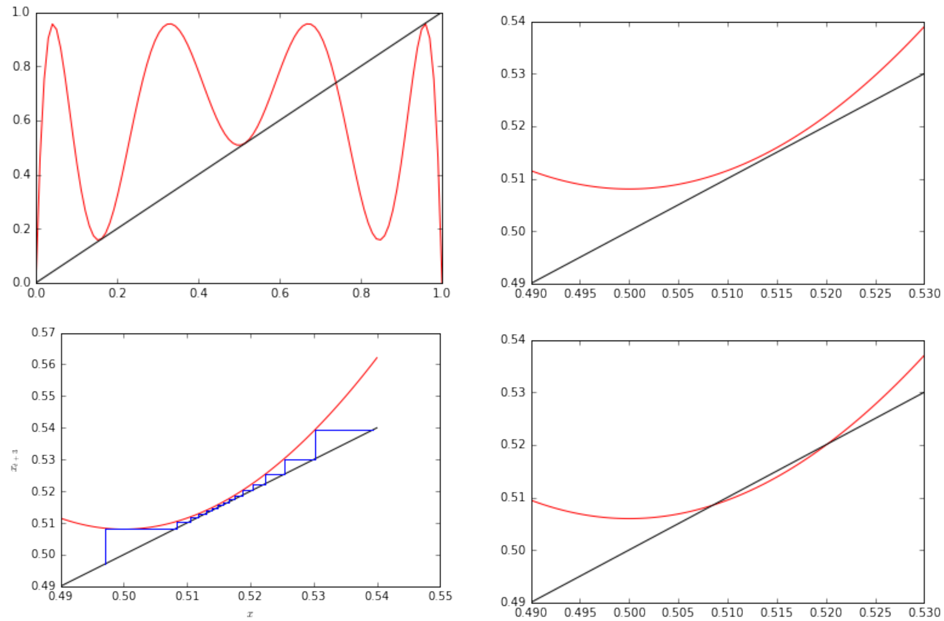

Figure 3: The top-left panel shows the logistic map applied three times with $\lambda = 3.828$; the top-right panel shows the map in the region around 0.5: it reveals that the third iteration comes close to intersecting the diagonal (and hence having a fixed-point, a three-cycle) but doesn't quite. The bottom-left panel shows the cobweb diagram for the three-map: it shows that for $x \approx 0.5$, the system tends to come back to a point close to where it was three iterations (of the single-map) ago, hence creating the appearance of a three cycle, but eventually travels out of this regime (when chaotic dynamics appear again). Finally, the bottom-right panel shows that when $\lambda = 3.829$, the three-map does intersect the diagonal, so there is a stable 3-cycle that emerges.