Harvesting a single natural population

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The simplest model for the growth of a population of organisms in a given environment is given by Malthus' law:

$$\dot{N}(t) = rN(t). \tag{1}$$

In this model (model I), $N(t)$ represents the number of individuals at time t and r is the population growth rate. This model, however, presents some inconveniences and is usually replaced by an improved version (model II) of the form:

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t)}{K}\right). \tag{2}$$

This is the *logistic equation.* The new parameter K is usually called the carrying capacity of the environment.

Pathological behavior of Malthus' law

For an arbitrary initial condition $N(0) = N_0 > 0$, the solution of (1) is

$$N(t) = N_0 e^{rt}. \tag{3}$$

So, we have only two possible behaviors:

- $r < 0$: the population monotonically decreases from N_0 to 0, being extincted.
- $r > 0$: the population monotonically increases without any upper limit.

Thinking in biological terms, such behavior is clearly a pathological one, not being observed in nature at all.

Notice that the quadratic term

$$-\frac{r}{K}N(t)^2$$

added in the Malthus' law to make up the logistic equation takes into account the effect of competition due to limitation of resources in the environment. As we shall see next when analyzing the fixed points of model II, the presence of such term prevents the population of growing up without any limit, thus fixing the aforementioned pathological behavior of model I.

Fixed points and stability analysis

On the following, we employ the notation $\dot{N} = f(N)$ to study the fixed points of models I and II.

Concerning the Malthus' law, we have $f(N) = rN$ and $f'(N) = r$, so that $N^* = 0$ is the only fixed point. Its stability depends on the signal of r: it is **stable** for $r < 0$ and **unstable** for $r > 0$. These two cases are illustrated in the figure below.

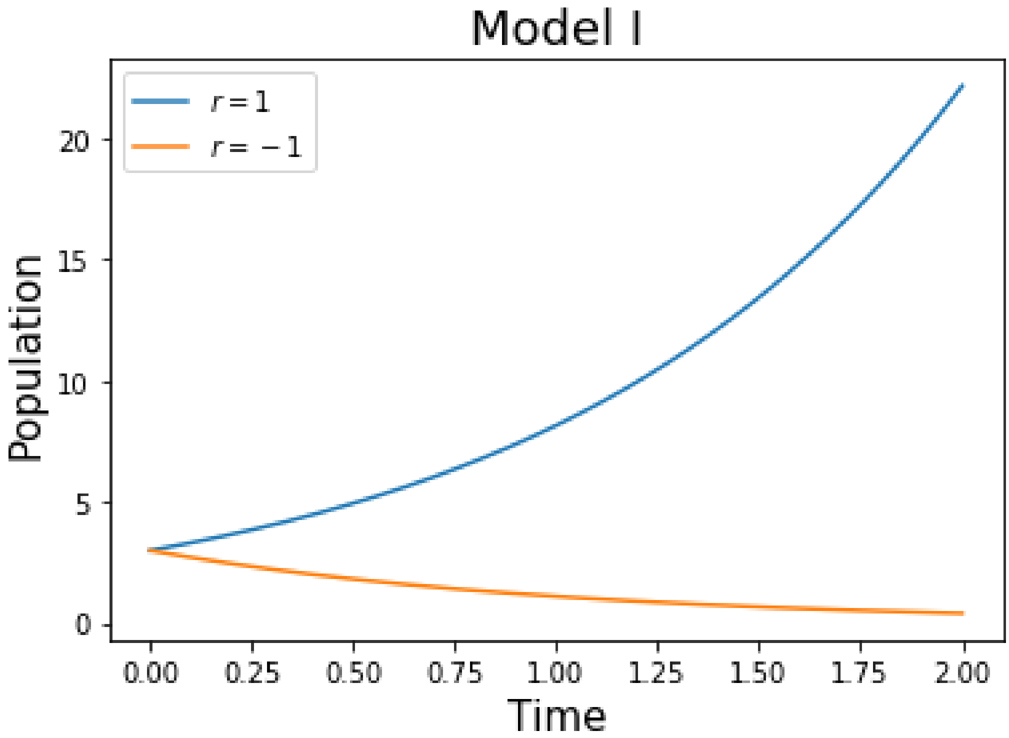

Figure 1: Representative cases of the Malthus'law

As for the logistic equation, we have $f(N) = rN\left(1 - \dfrac{N}{K}\right)$, so that the fixed points are

$$N_1 = 0 \text{ and } N_2 = K.$$

Since $f'(N) = r - \dfrac{2rN}{K}$, we have

$$f'(N_1) = r \implies N_1 \text{ is } \textbf{stable} \text{ if } r < 0 \text{ and } \textbf{unstable} \text{ if } r > 0;$$

$$f'(N_2) = -r \implies N_1 \text{ is } \textbf{unstable} \text{ if } r < 0 \text{ and } \textbf{stable} \text{ if } r > 0.$$

The interpretation is straightforward: assuming $r > 0$ (a population that grows naturally by consuming environmental resources), the population will reach a stationary state where its number will stabilize at the carrying capacity K. So, for a initial condition $N(0) > K$, we expect the population to decrease until it reaches the constant value $N = K$, whereas for $N(0) < K$ the population will increase until it reaches the stationary regime. Notice that this "self-regulatory" behavior is due to the limitation of resources (food, water, space, etc.). In the case where $r < 0$, we have a population that, somehow, naturally decreases even in the absence of the competition term; therefore, the extinction ($N = 0$) is the only possible stable scenario.

Let us consider the case $r > 0$, which is surely the more interesting one. Another qualitative feature to be pointed out is that there is essentially to different shapes for $N(t)$ when it approaches the carrying capacity K. Indeed, notice that the derivative $f'(N)$ changes its sign at $N = \frac{K}{2}$: for $N < \frac{K}{2}$, we have $f'(N) > 0$, and $f'(N) < 0$ for $N > \frac{K}{2}$. Thus, if the initial value of the population level satisfies $N(0) < \frac{K}{2}$, we will see a chance of concavity in the shape of $N(t)$, since until $N = \frac{K}{2}$ the population will be increasing with positive acceleration and, after this point, the acceleration is negative. Of course, this behavior will not be observed for initial conditions satisfying $N(0) > K$.

Next, we show some representative plots of the qualitative behavior of the logistic equation, for $K = 100$, $r = 0.2$ and different initial conditions.

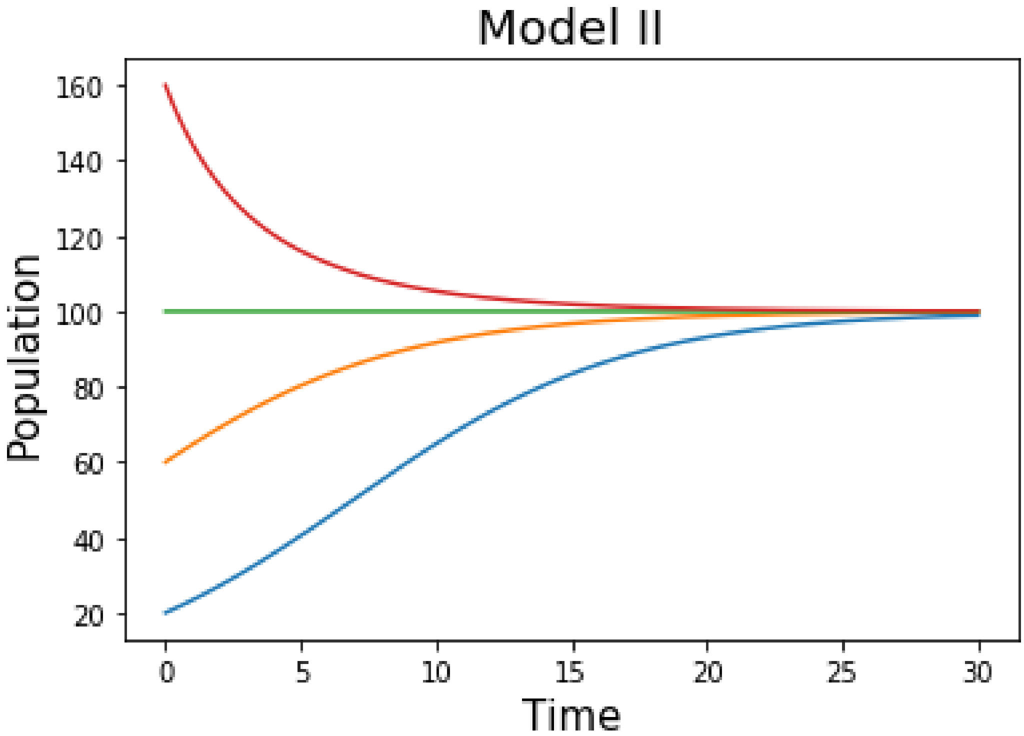

Figure 2: Representative cases of the logistic equation, assuming a population with a positive intrinsic growth rate ($r > 0$).

Notice that for $N(0) = 20 < \frac{K}{2} = 50$, we see a change on the concavity of $N(t)$. For all other choices of initial conditions with $N(0) > 50$, the population approaches the stationary level $N = K = 100$ with negative acceleration.

A model for harvesting fish

Although mathematically very simple, Model II is the basis for more elaborated models of population dynamics. Next, we will consider that N represents a population of fishes that can be harvested by humans. The effect of harvesting can be modeled by modifying Eq.(2) in various ways. Here, we consider (model III):

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t)}{K}\right) - EN(t). \tag{4}$$

The additional term $EN(t)$ is the harvesting yield per unit of time, being E a measure of the effort expended.

Here, the fixed points are the roots of the function

$$f(N) = rN\left(1 - \frac{N}{K}\right) - EN.$$

In order to determine the stability of the fixed points, we just need to study the sign of

$$f'(N) = r - E - \frac{2rN}{K}.$$

Fixed points:

- $N_1 = 0$: **stable** for $r < E$ and **unstable** for $r > E$.
- $N_2 = K\left(1 - \frac{E}{r}\right)$: **stable** for $r > E$. If $r < E$, we have $N_2 < 0$, what is a impossibility given the biological nature of the model. So, when $r < E$, $N = 0$ is the **only fixed point**, in which case it is stable.

Thus, we see that the harvesting effort E decreases the population of the stationary level by a factor of

$$1 - \frac{E}{r}$$

compared to what one has in model II. Also, if the harvesting effort is so large that it beats the intrinsic growth rate of the population, there will be no stable scenario other than extinction of the fish population. This is according to our biological intuition: too much harvesting may cause a fish population to be extinct. Equivalently, one can say that N_2 represents an "effective" carrying capacity of the environment due to the new effect of predation (harvesting).

As an illustrative example of such effect, we reproduce the same conditions of the graphics in figure 2 (that is: $K = 100$, $r = 0.2$, and the same initial conditions) with $E = 0.1$.

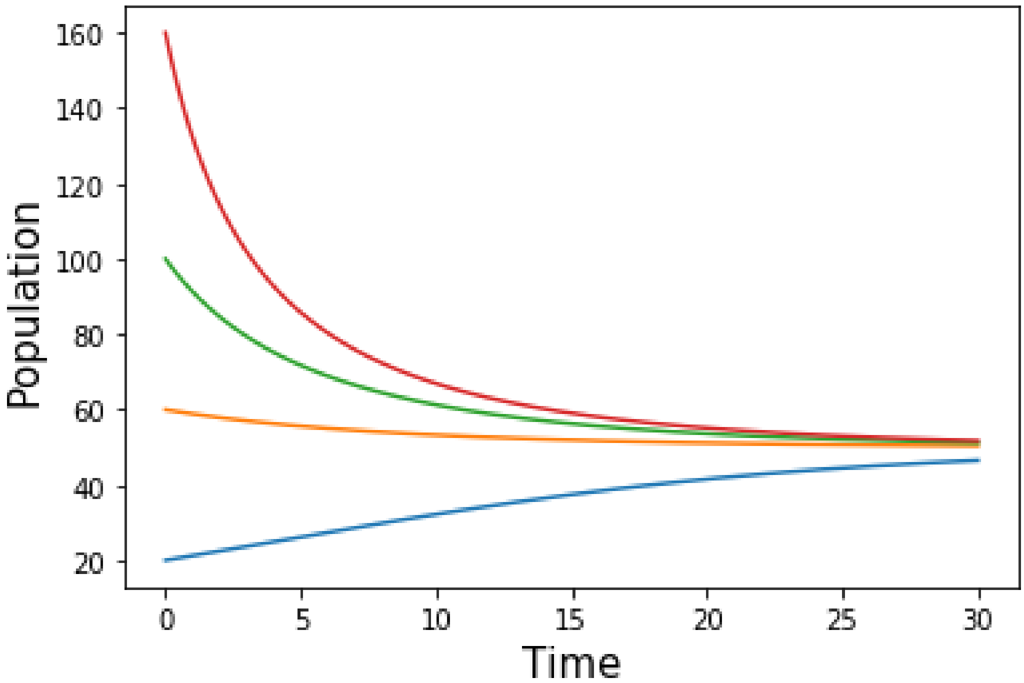

Figure 3: Fish population as a function of time (arbitrary units) for $r = 0.2$, $K = 100$ and $E = 0.1$.

Now, in order to further illustrate the present analysis, we make a plot of $N(t)$ for different values of the harvesting effort E. As before, we fix $K = 100$ and $r = 0.2$. As initial condition, we take $N(0) = 50$.

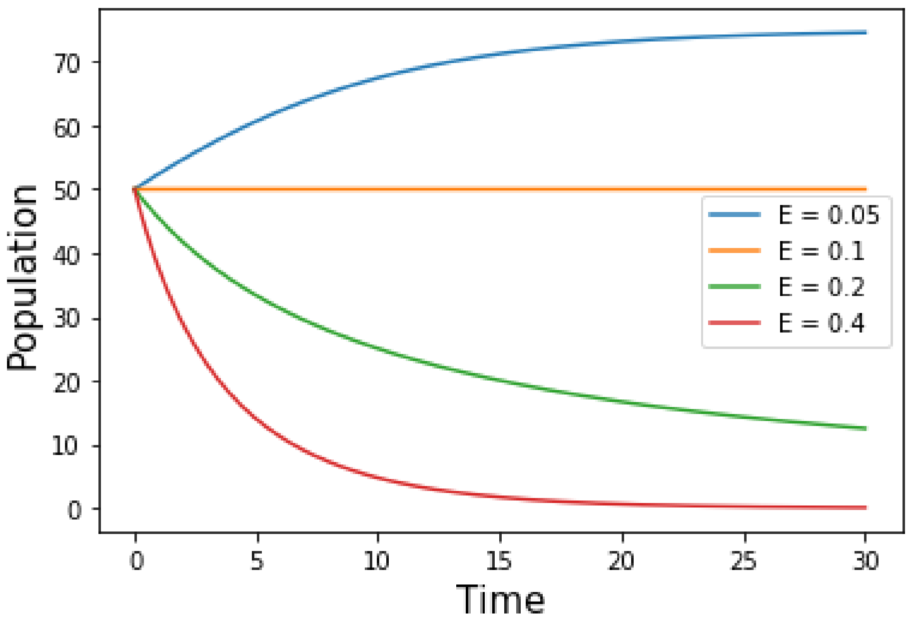

Figure 4: Fish population as a function of time (arbitrary units) for different values of the harvesting effort E. The other parameters are taken to be $K = 100$ and $r = 0.2$.

There is one more piece of analytical information that we can extract from model III. Indeed, notice that the harvesting yield in the steady state (assuming $E < r$) is given by

$$Y \equiv EN_2 = KE\left(1 - \frac{E}{r}\right). \tag{5}$$

It is easy to verify that Y has a maximum for

$$E = \frac{r}{2}.$$

So, in the context of the present model the optimal scenario for sustained harvesting occurs when the harvesting effort is half the intrinsic growth rate of the fish population. Moreover, in such optimal scenario we expect the fish population to stabilize at

$$N_2 = \frac{K}{2}.$$

Extra bonus

Consider now that our steadily harvested fishery is perturbed by a (small) external factor that takes it away from the stationary state. Let us do some stability analysis on the model III to see how and how fast the population react to such perturbation.

First of all, let us recall how one can perform the stability analysis on a generic system

$$\dot{x}(t) = f(x(t)).$$

Assume that this system has a fixed point $x = x^*$, with $f'(x^*) \neq 0$. Consider the perturbation

$$\eta(t) = x(t) - x^*.$$

The behavior of $\dot{x}(t) = \dot{\eta}(t)$ near such perturbation is well approximated by

$$\dot{\eta}(t) = f(\eta + x^*) \approx f(x^*) + f'(x^*)\eta = \eta f'(x^*).$$

Adapting this generic analysis to our case:

$$x^* = N_2 = K\left(1 - \frac{E}{r}\right) \quad (r > E),$$

$$f'(N) = r - E - \frac{2rN}{K} \implies f'(N_2) = E - r.$$

So, the behavior of a perturbation $\eta(t) = N(t) - N_2$ near the steadily harvesting scenario is described by

$$\eta(t) = \eta(t_0)e^{-(r-E)(t-t_0)}. \tag{6}$$

Just as expected, the population will eventually return to the stationary regime $N = N_2$, because $\eta(t) \to 0$ as $t \to \infty$. Moreover, since the perturbation is exponentially suppressed, it makes sense to define the characteristic time of recovering as

$$\mathrm{T} = \frac{1}{r - E}. \tag{7}$$

It is immediately seen that this time is smaller for a non-harvested population than for a harvested one. The ratio between the recovering times between the former and the latter is

$$\frac{\mathrm{T}_{E=0}}{\mathrm{T}_E} = 1 - \frac{E}{r}. \tag{8}$$