Mathematical Biology and Dynamical Systems. Lecture 1.

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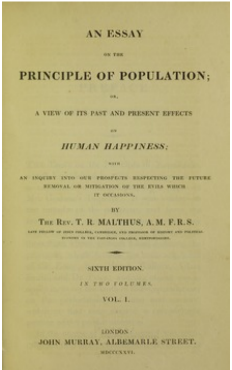
Malthusian and Logistic growth

Malthusian growth

Thomas Robert Malthus (1766-1834)
English clerical and scholar. Fellow of Jesus College (Cambridge) in 1794. In 1789, he took orders in the Church of England and became a curate (assistant cleric) at Oakwood Chapel in the parish of Wotton, Surrey.



AN ESSAY
ON THE
PRINCIPLE OF POPULATION;
OR,
A VIEW OF ITS PAST AND PRESENT EFFECTS
ON
HUMAN HAPPINESS;
WITH
AN INQUIRY INTO OUR PROSPECTS RESPECTING THE FUTURE REMOVAL OR MITIGATION OF THE EVILS WHICH IT OCCASIONS.
BY
THE REV. T. R. MALTHUS, A.M. F.R.S.

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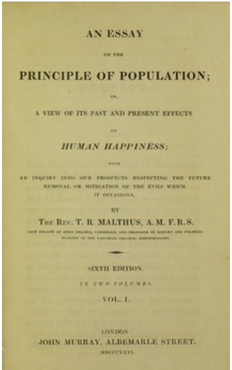

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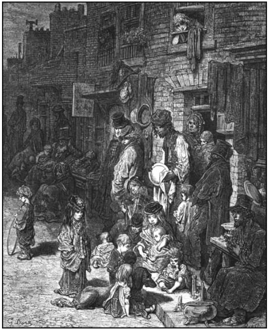
- *"An increase of nation's food leads to an improvement of the population. But, this is temporary since it implies a population growth which restores the initial per capita production level."*
- Mankind uses abundance to grow $\rightarrow$ Malthus trap.
- The power of population is much bigger than the power of Earth to produce subsistence for man.
- His idea was contrary to the 18th century common belief.
- L. Euler published in 1748 a treatise in which a population growth model of the form $P_{n+1} = (1 + x)P_n$ was assumed.

Malthusianism (population control)

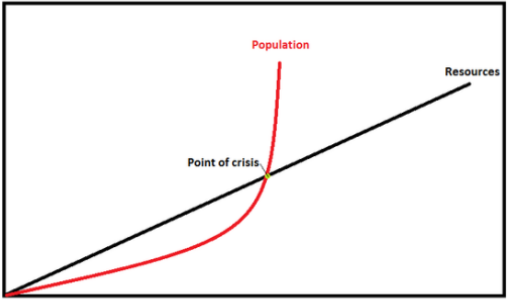
"The great Malthusian dread was that indiscriminate charity would lead to exponential growth in the population in poverty, increased charges to the public purse to support this growing army of the dependent, and, eventually, the catastrophe of national bankruptcy. Though Malthusianism has since come to be identified with the issue of general over-population, the original Malthusian concern was more specifically with the fear of over-population by the dependent poor."

Dan Ritschel, http://history.umbc.edu/facultystaff/full-time/daniel-ritschel/



Malthusianism (population control)

Exponential growth of population, linear growth of food. Moral restraints (abstinence, controlling marriages) or “positive checks” (diseases, starvation, war,...) resulting in Malthusian catastrophe.



Malthus' Basic Theory

Malthusian growth

Let $N(t)$ denote the population at time t. Then, the rate of change of N is modelled, in general, by

$$\frac{dN}{dt} = \text{births} - \text{deaths} \pm \text{migration}.$$

First model, suggested by Malthus in *Essay on the principle of population*, 1798. It only depends on birth and death rates (so no migration taken into account):

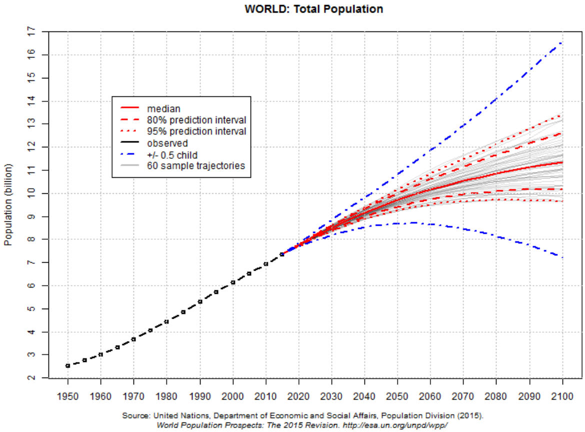
$$\frac{dN}{dt} = b\,N - d\,N \Rightarrow N(t) = N_0 \exp((b-d)t),$$

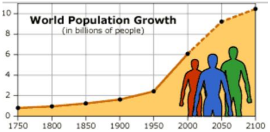
where N_0 is the initial condition and $b, d > 0$. It is clear that if $b > d$ it leads to exponential growth and if $b < d$ to extinction.
However it is an unrealistic approach, the growth estimates for the total world population from the 17th to 21st centuries point towards an exponential growth.

World population predictions

Date	Mid 17th century	Mid 19th century	1918–1927	1960	1974	1987	2000	2050	2100
Population in billions	0.5	1	2	3	4	5	6.3	10	11.2

United Nations median projections for the 21st century





Probabilistic projections obtained from http://esa.un.org/unpd/wpp/Graphs/Probabilistic/POP/TOT/.

Data fitting, statistical treatment,. . . see http://esa.un.org/unpd/wpp/ for a complete information.

Compare, for instance, predictions for Africa (really exponential) and Europe (decreasing from now on!).

Pierre François Verhulst (1804-1849)

- Belgian mathematician, doctor in Number Theory from the University of Ghent (1825).
- In his paper *Notice sur la loi que la population suit dans son accroissement*, Correspondence mathématique et physique 10, 113-121 (1838), he states the model

$$\frac{dN}{dt} = mN - nN^2.$$

  The limit

$$\lim_{t \to +\infty} N(t) = \frac{m}{n}$$

  is called by him as la limite supérieure de la population.
- Its main idea is that growth should possess a self-limiting mechanism to control it when it is too large.

The logistic growth

It is usually written as

$$\frac{dN}{dt} = r\,N\left(1 - \frac{N}{K}\right),$$

where

- r is the growth rate.
- K is the carrying capacity of the system.

and it is known as the logistic equation.

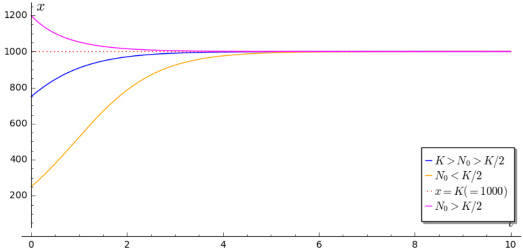
P. F. Verhulst
(1804–1849)

The continuous logistic growth: simple analysis

- $N = 0$ and $N = K$ are the only fixed points
- $f'(x) = r\,\left(1 - \frac{2\,N}{K}\right)$.
- $N = 0$ is a repellor because $f'(0) = r > 0$.
- $N = K$ is an attractor because $f'(K) = -r < 0$.
- Explicit solution of the ODE:

$$N(t) = \frac{K\,N_0}{N_0 + (K - N_0)e^{-r\,t}}.$$

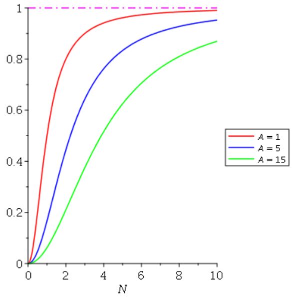
- All solutions (except $N = 0$) tend to K as $t \to +\infty$.



Observe the sigmoidal shape, ubiquitous in many mathematical models as a learning curve.

The continuous logistic growth: simple analysis

- If $N_0 > K$ solution decreases monotonically.
- If $N_0 < K$ it increases monotonically but qualitatively different if $N_0 > K/2$ or $N_0 < K/2$ (sigmoidal).
- The term sigmoidal was introduced by Michaelis and Mentem in 1913, and since then it has become standard.
- For a review on functional responses (in that case, for zooplankton feeding but also generalisable), see for instance, *Gentleman et al., Deep sea research II, 50, 2847–2875, (2003)*.



- Example (left) for $p(N) = BN^2/(A^2 + N^2)$ with $B = 1$.
- $p(N)$ has limit B for $t \to +\infty$. Reasonable since predation usually saturates for large values of N.
- They present, approx., a value N_c where $p(N)$ changes more abruptly. This threshold N_c depends on A.

Close models in discrete population dynamics

A quite general expression for them is of the form:

$$N_{t+1} = N_t F(N_t) = f(N_t), \qquad N_0 > 0.$$

Examples[1]:

- $F(N_t) = r \Rightarrow N_t = r^t\, N_0$ (*discrete Malthusian*).
- $f(N_t) = r\, N_t^{1-b}$ (*survival to breeding*).
- $F(N_t) = r\,(1 - N_t/K)$ (*discrete Verhulst, logistic*).
- $F(N_t) = \exp(r\,(1 - N_t/K))$ (severe death when overcrowded, *Ricker Model*).

Time steps can be thought of as delays so, should we expect oscillatory dynamics as well?

[1] [Murray, Mathematical Biology, Chapter 2]

The discrete logistic map

$$N_{t+1} = r\, N_t \left(1 - \frac{N_t}{K}\right), \qquad N_0 > 0.$$

"Perhaps we would all be better off, not only in research and teaching, but also in everyday political and economical life, if more people would take into consideration that simple dynamical systems do not necessarily lead to simple dynamical behaviour."

Robert May, 1976

Transcritical bifurcation in the logistic map

$$N_{t+1} = r\,N_t\left(1 - \frac{N_t}{K}\right), \qquad N_0 > 0.$$

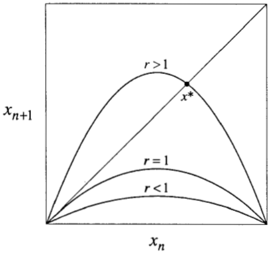
- If $t = n$ and $x_n = N_t/K$ for all $t, n \in \mathbb{N} \cup \{0\}$, then $f(x) = r\,x\,(1-x)$.

- Fixed points of f:

$$f(x) = x \Leftrightarrow r\,x(1-x) = x \Leftrightarrow x = 0 \text{ or } x = 1 - \frac{1}{r} =: x_r^*$$

- Transcritical bifurcation at $x = 0$

$$f'(0) = r = 1 \text{ when } r = 1.$$



Period doubling bifurcation

- Stability loss of $x^*(r)$ at $r = 3$:

$$f'(x^*(r)) = r(2/r - 1) = -1 \text{ when } r = 3.$$

- A stable 2-periodic orbit arises at $r = 3$ as $x^*(r)$ becomes unstable.

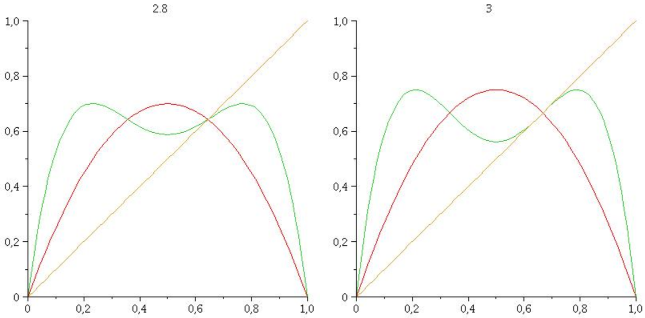


Figure: Graphs of $f(x)$ and $f^2(x) = f(f(x))$.

A cascade of period doubling bifurcations

Value of r	New period
$r_1 = 3$	2^1
$r_2 = 3.449\ldots$	2^2
$r_3 = 3.54409\ldots$	2^3
$r_4 = 3.5644\ldots$	2^4
$r_5 = 3.568759\ldots$	2^5
$\vdots$	$\vdots$
$r_\infty = 3.569946\ldots$	∞

A cascade of period doubling bifurcations

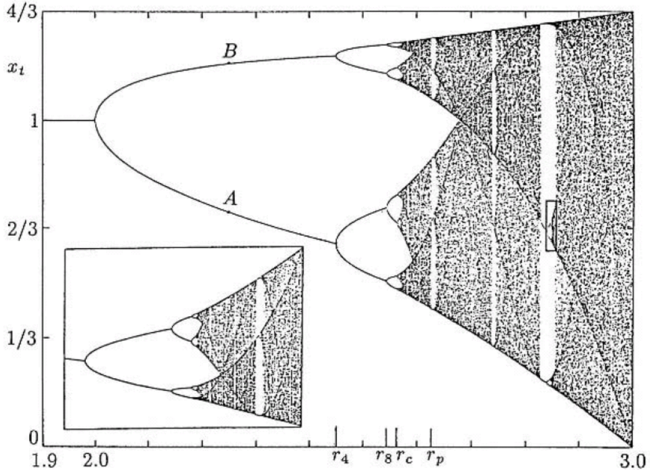


Figure: Can you hear the chaos? (https://www.youtube.com/watch?v=owq6xCFDbDQ)

Harvesting (and fisheries)

Harvesting (J.D. Murray, Section 1.6, pp. 30-35)

- **Target**: to develop an ecologically acceptable strategy for harvesting a renewable resource (fishes, plants, animals in general, ...). Even more, moved by the economical interest, we want to get the maximum sustainable yield with the minimum effort from our system.
- Seminal works: Clark (1976, 1985, 1990), Kot (2001), Plant and Mangel (1987), and many others.
- Simple model, suggested by Beddington and May (1977):

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - EN =: f(N), \tag{1}$$

  with $r, K, E > 0$.
- N is the quantity of population.
- r is the growth rate of the population and K is its carrying capacity.
- EN is the harvesting per unit time.
- E is called the fishing effort and in many situations it is denoted by qE', where q is called the catchability and E'. It is also known as the Schaeffer fishing model

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - qE'N.$$

- With no harvesting, that is $E = 0$, the logistic model has two equilibrium points:

$$N = 0 \quad \text{(repeller)} \qquad \text{and} \quad N = K \quad \text{(attractor)}$$

- If $E > 0$, the new non-zero equilibrium point is

$$N_h(E) = K\left(1 - \frac{E}{r}\right) \qquad \text{if} \quad E < r. \tag{2}$$

- This equilibrium gives rise to a yield

$$Y(E) := Y(N_h(E)) = EN_h(E) = EK\left(1 - \frac{E}{r}\right), \tag{3}$$

  which reaches its maximum value $Y_{\max}$ at $E_{\max} = \frac{r}{2}$, i.e. half the growth rate. Indeed,

$$Y_{\max} = Y(E_{\max}) = \frac{r}{2}K\left(1 - \frac{1}{2}\right) = \frac{rK}{4}, \qquad N_h(E_{\max}) = \frac{K}{2}. \tag{4}$$

- Which is the local stability of the point $N_h = N_h(E)$? Linearising around it we have

$$\frac{d}{dt}(N - N_h) \simeq f'(N_h)(N - N_h) = (E - r)(N - N_h), \tag{5}$$

  where $E - r < 0$ since $E < r$ (condition of N_h to exist).

- So $N = N_h$ is a local attractor (stable).

- Recovery time T_R: the time T_R satisfying the relation

$$N(t+T_R) - N_h(E) = \frac{N(t) - N_h(E)}{\mathrm{e}}, \tag{6}$$

for $0 < E < r$. Time needed to reduce its distance to N_h by a factor $\mathrm{e} = \exp(1)$.

- Since

$$\frac{d}{dt}(N - N_h) \simeq -(r-E)(N-N_h) \Rightarrow N(t) - N_h(E) \simeq \mathrm{e}^{-(r-E)t}$$

and (6) it follows that

$$\mathrm{e}^{-(r-E)(t+T_R)} \simeq \mathrm{e}^{-(r-E)t-1} \Rightarrow T_R(E) \simeq \frac{1}{r-E}. \tag{7}$$

- If no harvesting we have

$$T_R(0) \simeq \mathcal{O}\left(\frac{1}{r}\right).$$

- Comparing them:

$$\frac{T_R(E)}{T_R(0)} = \mathcal{O}\left(\frac{1}{1-\frac{E}{r}}\right), \tag{8}$$

which goes to ∞ as $E \to r^-$.

Which is, approximately, the recovery time factor in the case of the optimal harvesting effort $E_{\max} = \frac{r}{2}$?

- Observe that

$$T_R(E_{\max}) = \mathcal{O}\left(\frac{1}{r - E_{\max}}\right) = 2\,\mathcal{O}\left(\frac{1}{r}\right) = 2\,T_R(0).$$

- We express this recovery time in terms of the yield Y. Indeed, from (3) we have

$$\begin{aligned} Y(E) &= KE - \frac{K}{r}E^2 \Rightarrow \frac{E^2}{r} - E + \frac{Y}{K} = 0 \\ \Rightarrow & \quad E = \frac{1 \pm \sqrt{1 - \frac{4}{r}\frac{Y}{K}}}{2/r} = \frac{1 \pm \sqrt{1 - \frac{Y}{Y_{\max}}}}{2/r}, \end{aligned}$$

since $Y_{\max} = Kr/4$.

- So

$$\frac{E}{r} = \frac{1 \pm \sqrt{1 - \frac{Y}{Y_{\max}}}}{2}$$

and then

$$\frac{T_R(E)}{T_R(0)} = \mathcal{O}\left(\frac{1}{1 - \frac{E}{r}}\right) \simeq \frac{1}{1 - \frac{1}{2}\left(1 \pm \sqrt{1 - \frac{Y}{Y_{\max}}}\right)} = \frac{2}{1 \mp \sqrt{1 - \frac{Y}{Y_{\max}}}}. \tag{9}$$

- Notice that $T_R(E = 0) = T_R(Y = 0)$ so it can also be written as

$$\frac{T_R(Y)}{T_R(0)} \sim \frac{2}{1 \pm \sqrt{1 - \frac{Y}{Y_{\max}}}}. \tag{10}$$

- Next Figure 3 shows the two branches of $T_R(Y)/T_R(0)$:

$$L_{\pm} = \frac{2}{1 \pm \sqrt{1 - \frac{Y}{Y_{\max}}}}, \tag{11}$$

as a function of the rate $Y/Y_{\max}$.

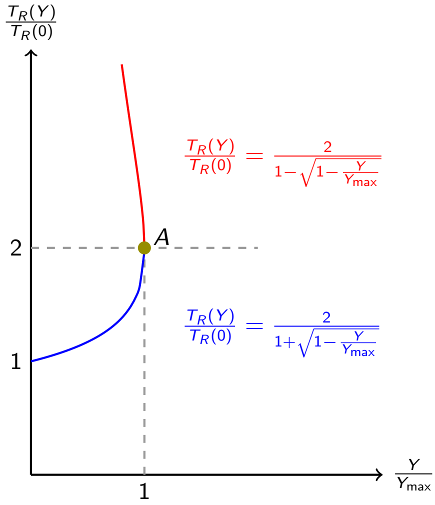


Figure: The two branches $L_\pm$ given at (11) of $T_R(Y)/T_R(0)$ in terms of $Y/Y_{\max}$.

Let us analyse the behaviour of recovery time of the solutions in terms of the harvesting E. Remember that the steady state of the harvested model, Y, can be graphically determined:

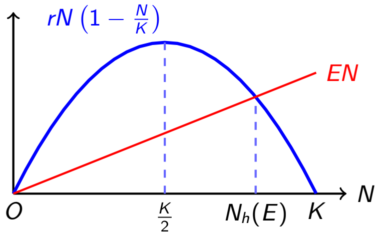
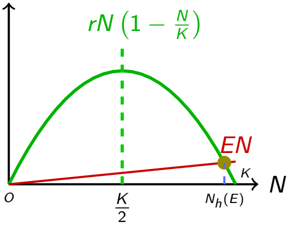
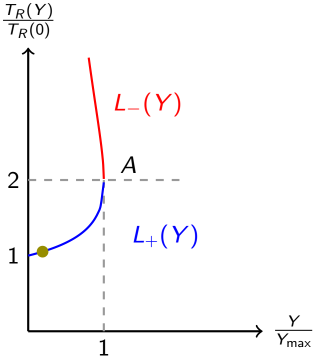


Figure: Graphic determination of the steady state Y in the harvested model: it is given by the intersection of the line $y = EN$ and the parabola $y = rN\left(1 - \dfrac{N}{K}\right)$.



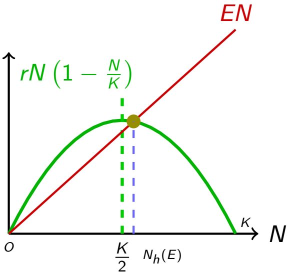
E =0.1



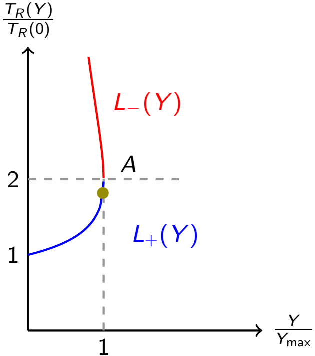
Consequences:

- For $E \sim 0$ we have $N_h(E) \sim K$. In particular, $N_h(E) > \frac{K}{2} = N_h(E_{\max})$. Moreover, since $T_R(E)/T_R(0) \sim 1$ and so

$$\frac{Y}{Y_{\max}} \sim 0 \qquad \text{and} \qquad \frac{T_R(Y)}{T_R(0)} \sim 1.$$



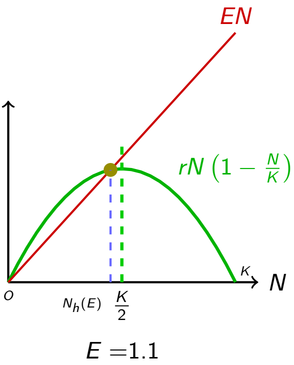
E =0.9

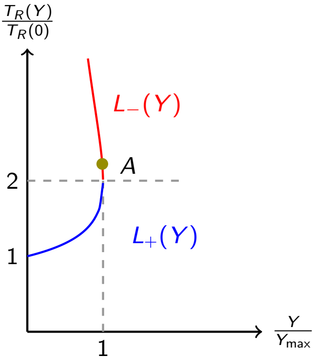


As we increase E:

(i) $N_h(E)$ decreases approaching $N_h(E_{\max}) = \frac{K}{2}$.

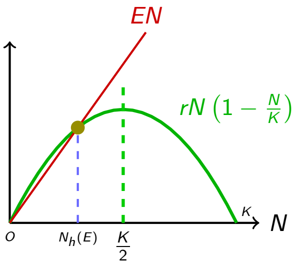
(ii) Consequently, $\frac{T_R(Y)}{T_R(0)}$ tends to the point A, but still in the L_+-branch.



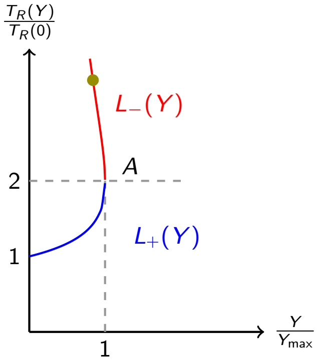


- Further increasing E leads to an equilibrium $N_h(E)$ smaller than $K/2$. Again the recovery time rate $\frac{T_R(Y)}{T_R(0)}$ increases but now on the branch L_-. Indeed, since $E > E_{\max} = \frac{r}{2}$, it follows that

$$T_R(E) \sim \frac{1}{r-E} > \frac{1}{r/2} = \frac{2}{r} \sim 2T_R(0) \Longrightarrow \frac{T_R(E)}{T_R(0)} > 2 \Longrightarrow \frac{T_R(Y)}{T_R(0)} > 2.$$



$E = 1.4$



- Hence, as E continuous increasing we get $N_h \to 0^+$ and so $\frac{Y}{Y_{\max}} \to 0^+$ (since $Y = EN_h$). Consequently,

$$1 - \frac{Y}{Y_{\max}} \to 1^+ \Longrightarrow \frac{T_R(Y)}{T_R(0)} = \frac{2}{1 - \sqrt{1 - \frac{Y}{Y_{\max}}}} \to +\infty.$$

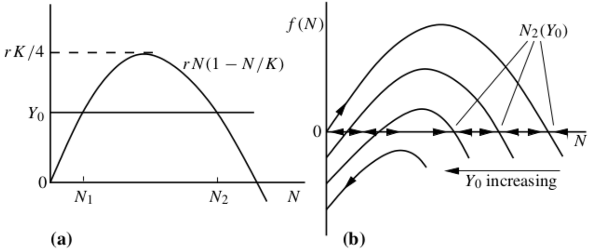
That is, the recovery time grows enormously!!

Is a constant harvesting a general better strategy?

This alternative model was posed by Brauer and Sánchez [3]. They consider a constant yield Y_0:

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - Y_0.$$

New equilibria can be easily determined graphically.



- As Y_0 tends to $rK/4$, the maximum sustainable yield, the solution becomes even more sensitive than in the previous model. Indeed, any small fluctuation can make $Y_0 > rK/4$ and, therefore, the origin (extinction) becomes the unique steady state. Moreover, it is a global attractor.

- Even if $Y_0 < rK/4$ and N is below the (unstable) equilibrium N_1 (so, N small), we have that N is small and essentially

$$\dot{N} \sim -Y_0 \Rightarrow N(t) = -Y_0 t + N(0),$$

This implies that the population N dissapears in finite time

$$T_{\text{dissap}} = \frac{N(0)}{Y_0}.$$

- Thus, recovery time has only sense for the (locally attractor) steady state

$$N_2(Y_0) = \frac{K}{2}\left(1 + \sqrt{1 - \frac{4Y_0}{Kr}}\right),$$

which exists if $Y_0 < rK/4$. The linearised system around N_2 is

$$\frac{d}{dt}(N - N_2) \simeq -(N - N_2) r \sqrt{1 - \frac{4Y_0}{Kr}} \Longrightarrow \frac{T_R(Y_0)}{T_R(0)} = \frac{1}{\sqrt{1 - \frac{Y_0}{Y_{\max}}}},$$

with $Y_{\max} = rK/4$. That is,

$$\frac{T_R(Y_0)}{T_R(0)} \to +\infty \qquad \text{as} \qquad Y_0 \to Y_{\max}.$$

So, this strategy is even more sensitive than the precedent one and it is not really very convenient.

Density-dependence growth: the Allee effect

The θ-logistic equation

- Given by
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)^{\theta},$$
with $\theta > 1$, introduced by Gilpin and Ayala in 1973.
- It represents a no declining in the per capita population growth until it reaches a level close to carrying capacity K, followed by a fast decline (see Figure 34).

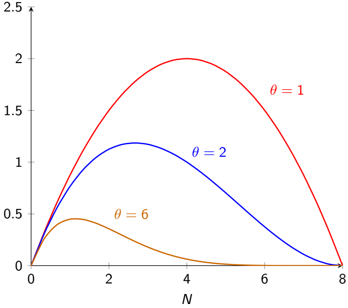


Figure: Graphs of θ-logistic function $rN\left(1 - \frac{N}{K}\right)^{\theta}$ for $r = 1$, $K = 8$ and several values of θ. Remember that $\theta = 1$ corresponds to the usual logistic function.

The Allee effect

It was introduced by the zoologist and animal ecologist Warder Clyde Allee (1885-1955), from the University of Chicago.
He was interested in the study of group behaviour of animals.
At the moment he presented his theory, two were the general beliefs among biologists:

- Large population size is important against extinction and enemies (Charles Darwin).
- Intraspecific competition does not decrease with population size: Malthus principle + logistic model.

Allee observed that, in many species, it was undercrowding and not competition the reason that limited population growth.

"In general, an Allee effect can be defined as a positive relationship between mean individual fitness and population size or density (hereafter population size), generally occurring in small populations (Stephens, Sutherland, & Freckleton, 1999). More specifically, Allee effects occur when there are beneficial interactions among individuals that cause the per capita population growth rate to increase with the number of individuals. Conversely, if the number of individuals decreases, they suffer from fewer or less efficient interactions and the per capita population growth rate decreases. The critical population size below which the per capita population growth rate becomes negative is called the Allee threshold. A major consequence of the Allee effect is that populations falling below the Allee threshold become even smaller, thereby entering into a positive feedback loop that can ultimately lead to their extinction ..."

Courchamp, Clutton-Brock, & Grenfell, 1999.

Aggregation seems to have positive effects on the survival of some species. The most common Ecological mechanisms for Allee effect to exist are (see, for instance [1])

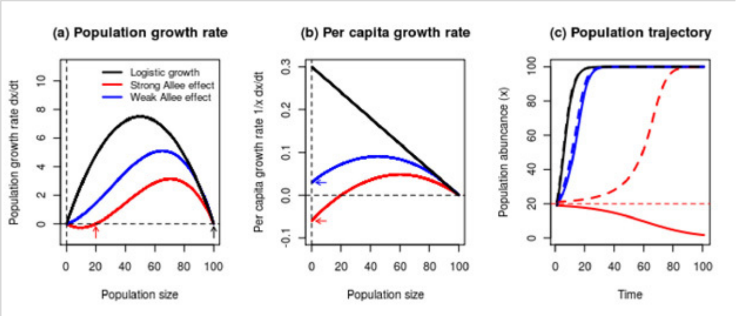
- Mate limitation.
- Cooperative defense: schools of sardines, flocks of starlings, ...
- Cooperative feeding: African wild dogs that hunt together, ...
- Environmental conditioning / habitat alteration: marine nutrients carried by spawning salmons when they migrate along streams to reproduce, ...

Figure: School of sardines.

In general it can be represented by the mathematical model:

$$\frac{dN}{dt} = rN\left(\frac{N}{A} - 1\right)\left(1 - \frac{N}{K}\right) \tag{12}$$

where A is called the Allee threshold or critical population size, and K is the carrying capacity.



Suggested homework: To study harvesting in a population undergoing Allee effect like, for instance, in equation (12)

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